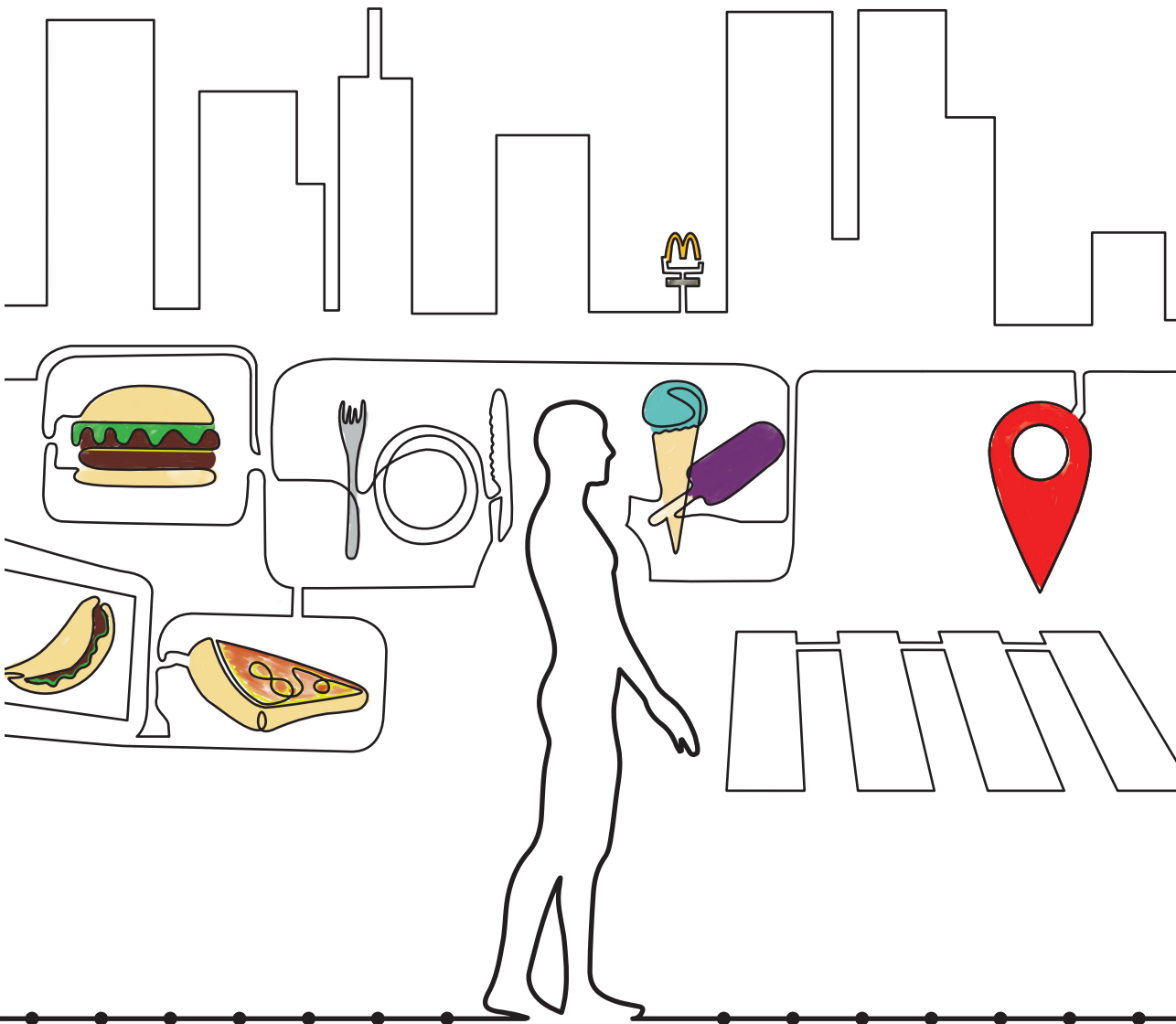


Foraging Minds in Modern Food Environments

A High-calorie Bias in
Human Spatial Memory and its
Implications for Eating Behavior



Rachelle de Vries

Propositions

1. Your mind is fundamentally wired to better remember locations of calorie-rich foods, whether you like it or not.
(this thesis)
2. To promote healthy eating behavior, it would be a more effective strategy to target the translation (rather than the expression) of the high-calorie bias in human spatial memory.
(this thesis)
3. Getting in direct contact with your target population of interest will enhance the quality of your research.
4. To facilitate best scientific practices, a separate metric for open science efforts should be publicly attached to a researcher's profile.
5. To encourage a constructive and fair peer review process, reviewer identities should be mandatorily disclosed during review and published upon article acceptance (Ross-Hellauer *et al.*, 2017; Walker & da Silva, 2015).
6. In advancing a professional career, the importance of social skills will outweigh content expertise, even in highly technical jobs.
7. The body positivity movement poses a threat to public health.

Propositions belonging to the PhD thesis entitled:

Foraging Minds in Modern Food Environments: A High-calorie Bias in Human Spatial Memory and its Implications for Eating Behavior

Rachelle de Vries

Wageningen, August 30, 2021

Foraging Minds in Modern Food Environments:

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Foraging Minds in Modern Food Environments:

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Implications for Eating Behavior

Rachelle de Vries

Thesis

submitted in fulfilment of the requirements for the degree of doctor

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Prof. Dr A.P.J. Mol,

in the presence of the

Thesis Committee appointed by the Academic Board

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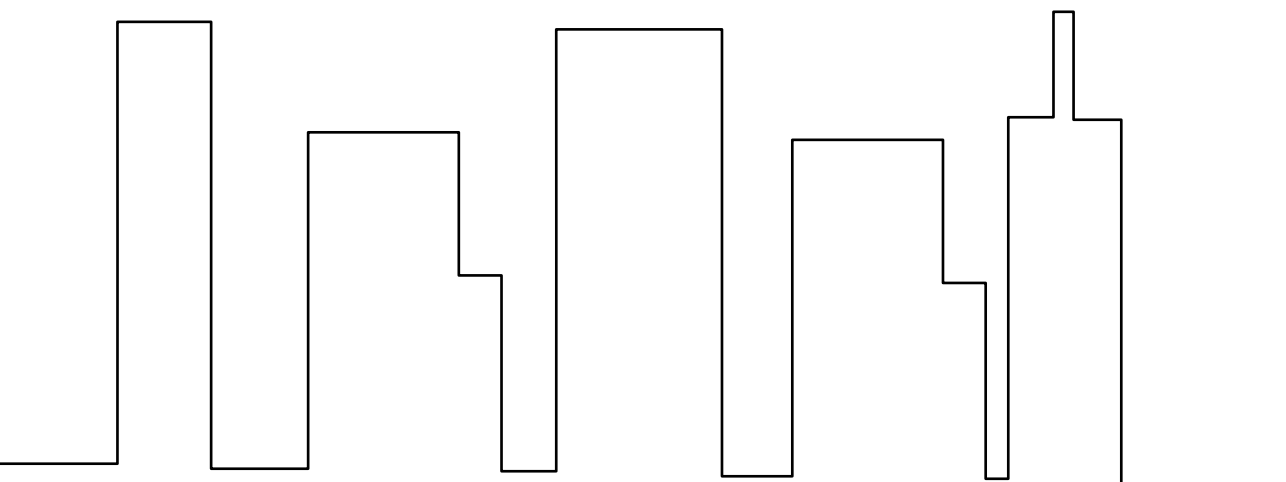
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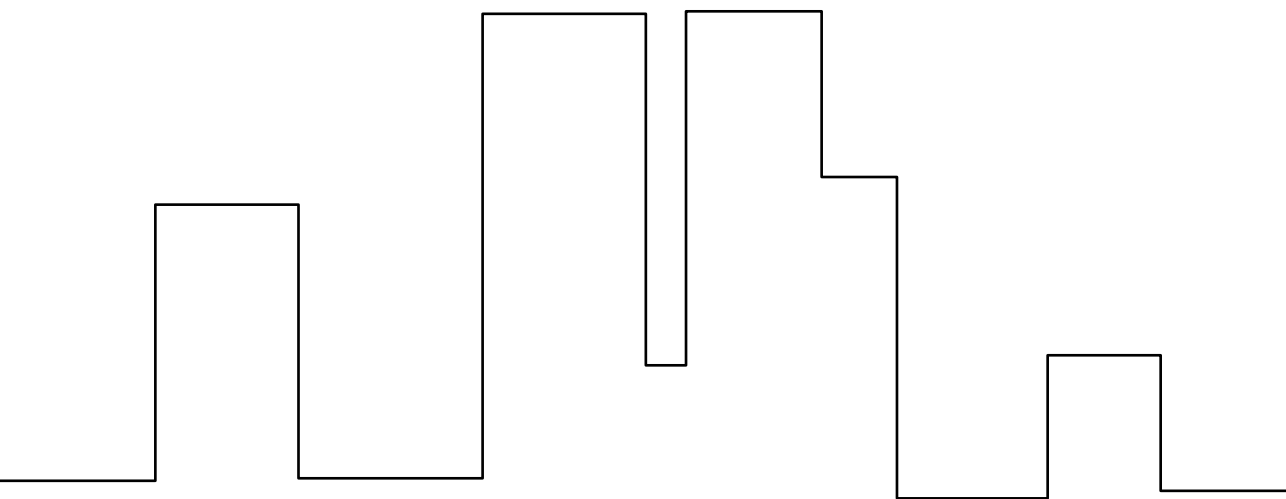
To Dad,

*Your loving memories will forever be a beacon of light
guiding my path.*

Table of Contents

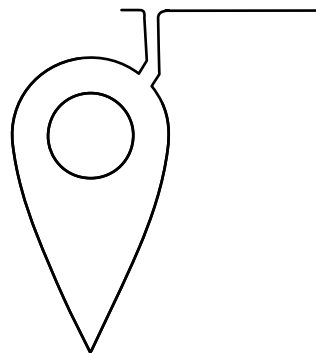
Chapter 1	9
General Introduction	
Chapter 2	25
Foraging minds in modern environments: High-calorie and savory-taste biases in human food spatial memory	
Chapter 3	63
Human spatial memory implicitly prioritizes high-calorie foods	
Chapter 4	75
Locating calories: Does the high-calorie bias in human spatial memory influence how we navigate the modern food environment?	
Chapter 5	107
Wired for harsh food environments: Human spatial memory favors the effortless location and consumption of high-calorie foods	
Chapter 6	139
Human spatial memory is biased towards high-calorie foods: A cross-cultural online experiment	
Chapter 7	163
General Discussion	
References	185
Summary	215
Acknowledgements	221
About the Author	231





Chapter 1

General Introduction



"If memory evolved, sculpted by the processes of natural selection, then its operating characteristics likely bear the "footprints" of ancestral selection pressures"

- Nairne & Pandeirada (2008b, p.239)

1.1. Introduction

Obesity is one of the largest global health threats of our time and its prevalence continues to rise unabatedly since the 1980s, with recent figures estimating that 39% of adults worldwide were overweight and 13% were obese as of 2016 alone (Swinburn *et al.*, 2019, World Health Organization, 2020). On the individual level, obesity represents a debilitating condition and is a precursor for many comorbidities such as cardiovascular diseases and diabetes (Ezzati *et al.*, 2002; Prospective Studies Collaboration, 2009; World Health Organization, 2020). On a societal level, the management of obesity and its comorbidities incurs a steep price for public spending, with economic costs totaling up to 8% of a country's overall healthcare expenditures (Kortt *et al.*, 1998). Furthermore, as recently demonstrated by the COVID-19 pandemic, a higher BMI is an independent risk factor for disease severity and mortality (Hamer *et al.*, 2020; Petrilli *et al.*, 2020), and a large number of individuals with excessive body weight likely renders countries less successful at containing the spread of infection (Green & Beck, 2017; Kassir, 2020; Sattar *et al.*, 2020). There is strong consensus that an individual's diet, or energy intake, plays a fundamental (yet modifiable) role in the etiology and maintenance of overweight and obesity (World Health Organization, 2004; World Health Organization, 2020). A substantial body of evidence indicates that a diet rich in (saturated) fats, sodium, and added sugars (but poor in fruits, vegetables, and legumes) is tied to sustained weight gain in individuals (Hill, 2006; World Health Organization, 2004). The reduction of excess body weight through tackling unhealthy dietary patterns thus assumes a high ranking on national health agendas worldwide (World Health Organization, 2004).

In turn, it is generally agreed upon that the modern calorie-laden food environment is to be held accountable for the sharp universal rise in unhealthy diets (Lakerveld *et al.*, 2018; Swinburn *et al.*, 2011; Swinburn *et al.*, 2019). Longitudinal deteriorations in dietary quality – as well as gains in body weight – witnessed in the past 40 to 50 years worldwide has largely paralleled transitions in the global food system towards an increased supply of processed energy-dense foods (Finucane *et al.*, 2011;

Imamura *et al.*, 2015; Swinburn *et al.*, 2011). At lower levels, this drastic global “nutrition transition” has manifested as adverse changes in the physical structure of *micro* food and eating environments (e.g. supermarkets and other food retail establishments), to include a wider variety of cheap, palatable, and convenient calorie-rich yet nutrient-poor foods (Lake & Townshend, 2006; Strong *et al.*, 2008; Swinburn *et al.*, 2011). Consequently, an enhanced (in-store) availability and accessibility to such items within a food retail environment – as well as in the quantity and proximity to unhealthy food retailers (e.g. fast food outlets) in one’s local built environment – creates circumstances conducive to the passive overconsumption of calories (Hollands *et al.*, 2019; Pitt *et al.*, 2017; Strong *et al.*, 2008). From this theoretical standpoint, overeating is conceptualized as a normal response to an abnormal food environment (Egger & Swinburn, 1997; Lakerveld *et al.*, 2018).

However, the emerging evidence is much more nuanced, as *not* everyone consumes excessive amounts of calories in response to abundant food cues, suggesting that large differences exist in how individuals navigate unhealthy food surroundings. A host of factors have been identified in literature that moderate individual vulnerabilities to an increased availability and accessibility to energy-dense foods. For instance, an individual’s competence in employing self-regulation strategies (e.g. reducing confrontation with tempting food cues; distracting oneself from temptations) can act as a protective buffer against easy access to high-calorie foods, either directly (de Vet *et al.*, 2013) or by attenuating one’s psychological sensitivity to these cues in the environment (Stok *et al.*, 2015). A greater inhibitory control capacity may also support healthier food navigation by terminating impulsive (prepotent) behavioral responses to encountered high-calorie foods, and affording individuals the ability to act in line with their long-term healthy eating goals (Appelhans *et al.*, 2011; Batterink *et al.*, 2010; Nederkoorn *et al.*, 2010). Conversely, other individual-level factors can negatively interact with aspects of the modern food environment and lead to undesirable behavioral outcomes. These include one’s predisposition for external eating (van Strien *et al.*, 1986), which has been shown to facilitate attentional detection of palatable food cues (Hou *et al.*, 2011), and positively correlate with overeating (Davis *et al.*, 2007) as well as BMI (van Strien *et al.*, 1985). Likewise, a greater sensitivity to rewarding cues (i.e. reward sensitivity) is documented to bias visual attention towards appetizing foods

(Tapper *et al.*, 2010), induce craving for (palatable) foods (Franken & Muris, 2005), and heighten preferences for high-fat and high-sugar products (Davis *et al.*, 2007).

Having said that, this thesis entertains the novel notion that a promising yet overlooked component linking an omnipresence of energy-dense foods to suboptimal diets lies in our extended evolutionary history as hunter-gatherers. Namely, we posit that individual differences in susceptibilities to the current “obesogenic” food environment may also (partially) be attributed to a cognitive adaptation that evolved for optimal foraging within harsh ancestral food landscapes: a prioritization – or “bias” – in human spatial memory for high-calorie foods (Allan & Allan, 2013; New *et al.*, 2007b). To this end, the remainder of the General Introduction is devoted to outlining the conceptual underpinnings of this thesis. We firstly touch upon the existence and theory behind evolved foraging-based adaptations in human memory (section **1.2**). After, we focus specifically on how an apparent “high-calorie bias” in human spatial memory is expected to impact on individuals’ eating behavior (e.g. food choice and dietary intake; section **1.3**), before concluding with the aim and overview of this thesis (section **1.4**).

1.2. The Adapted Mind: The Case for Foraging-related Adaptations in Human Memory

1.2.1 Traditional versus adaptive accounts of human memory

Historically, disciplines within the cognitive sciences have been reluctant to acknowledge evolutionary influences on the organization and workings of the human mind (Tooby & Cosmides, 2005; Tooby *et al.*, 2005; see Fodor, 2000 for a commentary on the “superfluous” nature of evolutionary theory for human cognition). Traditional memory frameworks (e.g. Craik & Lockhart, 1972) thus tend to focus on structural explanations for *how* certain events are better remembered than others, rather than functional explanations for *why* these mnemonic effects occur in the first place (Nairne & Pandeirada, 2008b; Nairne & Pandeirada, 2010). For instance, a lot of research has been conducted on the proximal mechanisms underlying how visually representing an item improves its retention (e.g. mental elaboration; Tulving & Craik, 2000), but little attempt has been made to understand why memory shows such sensitivities to visual content (Nairne & Pandeirada, 2008b; Nairne & Pandeirada, 2010). However, by incorporating more functional analyses of cognitive processes – as well as recognizing

the important role evolutionary (fitness-based) principles plays – human memory operations will be better understood and ecologically-meaningful insights can be obtained (e.g. developing encoding techniques better suited to natural processing tendencies of memory systems) (Nairne & Pandeirada, 2008b; Nairne & Pandeirada, 2010; Tooby & Cosmides, 2005).

The crux of contemporary memory theory is that recall performance across situations depends predominantly on “general-purpose” learning mechanisms that do *not* differentiate between the types of information to be encoded (i.e. content-insensitive mechanisms; Nairne, 2010; Nairne & Pandeirada, 2010; Tooby & Cosmides, 2005). That is, encoded events are assumed to be treated equally and the likelihood of correct recall is mainly dependent upon factors external to the encoded information itself, such as the quality of the retrieval environment (Tulving & Thomson, 1973). Consider the widely-used “levels of processing” framework (Craik & Lockhart, 1972), which stipulates that one will better recall information related to an object (e.g. eating an apple at a certain location) with an increasing familiarity with that object (e.g. frequency of apple consumption), due to an enhanced ability to generate rich memory traces of the object that are likely to match retrieval cues present during recall. As such, memory performance is simply a reflection of the relative “encoding-retrieval match”, or degree of overlap in the constellation of cues present between encoding and retrieval environments (Tulving & Thomson, 1973).

Conversely, proponents of an adaptive account of human cognition emphasize that our capacity to remember did not evolve in a vacuum (Nairne, 2010; Nairne & Pandeirada, 2008b; Tooby & Cosmides, 2005). Rather, human memory systems – much like other biological systems – were shaped by natural selection pressures to solve fitness-relevant problems, especially those encountered in the ancestral environments in which we evolved (Nairne, 2010). It follows then that memory mechanisms *should* adaptively show sensitivity and preference for content that carried fitness-significance throughout our evolutionary history (Nairne, 2010; Nairne & Pandeirada, 2008b). Examples of such content include – but are not limited to – locations of (edible versus inedible) foods, water, and shelter; and migratory patterns of predators and prey (Nairne & Pandeirada, 2008b). Indeed, instances in which memory faculties prioritized stimuli with survival importance – irrespective of personal expertise with or present utility of the encoded information – are increasingly documented (e.g. animacy effects on

episodic memory; Nairne & Pandeirada, 2008a; Nairne *et al.*, 2017), and have been generalized to the domain of visual attention (e.g. attentional “tripwires” for predator detection; LoBue & DeLoache, 2008; New *et al.*, 2007a). Importantly, it is this adaptive perspective on human memory that forms the primary conceptual point-of-departure of this thesis.

1.2.2 The Paleolithic prologue: Optimal foraging as a central adaptive problem in ancestral food environments

Although calorie-rich surroundings are commonplace nowadays, such foraging circumstances are unprecedented within the broader context of human evolutionary history. For around 99% of our evolutionary trajectory – spanning the entire Paleolithic era from roughly 2.5 million years to 12,000 years ago – our ancestors were hunter-gatherers inhabiting a highly complex and variable food environment (Adler *et al.*, 2006; Stiner & Bar-Yosef, 2005; Stiner & Kuhn, 2009; Ulijaszek, 2002). Such environments were defined by extreme fluctuations in energy supply, or periodic cycles of “feast and famine”, as spatiotemporal distributions of foods were tightly coupled with seasonal variations (Chakravarthy & Booth, 2004; Ulijaszek, 2002). As a result, physical activity and food procurement were inextricably linked, in that early humans had to engage in intensive foraging activities to acquire sufficient nutrition (Chakravarthy & Booth, 2004; Cordain *et al.*, 1998; Eaton, 2006; Eaton *et al.*, 1997). Indeed, the average ancestral hunter-gatherer was estimated to expend approximately 3000 kilocalories (kcal) of energy per day (Cordain *et al.*, 1998; Eaton, 2006). In addition, there were opportunity costs involved with foraging: time was a fixed resource that had to be shared with other adaptive nonforaging activities (Winterhalder, 1981), and hunter-gatherers faced heavy predation risks (Hart & Sussman, 2008). Thus, the successful acquirement of high-quality nutritional resources – once they became available – likely formed a central adaptive problem in the bulk of our evolutionary past, as it represented a recurring task that critically affected the survival and reproduction of our hunter-gatherer predecessors (Cosmides & Tooby, 1997; MacArthur & Pianka, 1966).

Optimal foraging theory states that selection pressures introduced by such harsh ancestral food habitats would have favored behavioral strategies that maximize the net energy gained per unit time spent on foraging (Schoener, 1971; Winterhalder, 1981). In other words, the central adaptive problem of optimal foraging would select for behaviors (and underlying cognitive mechanisms) that lead to the energy-efficient

procurement of food resources (Hill *et al.*, 1987; Schoener, 1971). In turn, an increased efficiency in the rate of energy capture is expected to enhance individual fitness, as more net energy is made available for performing adaptive tasks (e.g. provisioning offspring) (Gaulin & Konner, 1977; Pyke *et al.*, 1977; Smith, 1979; Winterhalder, 1981). This optimal foraging principle of energy maximization has demonstrated good validity for predicting subsistence patterns of numerous animal species, as well as contemporary hunter-gatherer societies (Hill *et al.*, 1987; Krebs *et al.*, 1983; Smith *et al.*, 1983).

1.2.2.1 Foraging-relevant sensory modalities

The sensory modalities of vision, olfaction, and taste are deeply embedded in the foraging activities of human and various non-human primate species (see Dominy *et al.*, 2001 and McCrickerd & Forde, 2016 for reviews). Below, we briefly recap the importance of each modality for the respective processes of food search and localization, food choice, and food consumption.

Vision is considered a “distant” sense that acts as the first point of contact between an individual and a potential food item, drawing attention to relevant objects from long distances (McCrickerd & Forde, 2016; Schifferstein *et al.*, 2013). Upon visually appraising a food, individuals rapidly construct beliefs and expectations about its corresponding properties (i.e. sensory and hedonic profiles), relying on past experiences with (similar) products and their post-ingestive consequences (Deliza & MacFie, 1996; van der Laan *et al.*, 2011). Indeed, overlapping brain regions are activated when viewing pictures of foods as when tasting them (Simmons *et al.*, 2005), and previous research shows that mainly vision-derived expectations inform individuals during moments of food choice (Schifferstein *et al.*, 2013). Interestingly, visual cues (e.g. packaging labels) shape not only expectations but also *actual* perceptions of a food’s qualities upon consumption, including its taste intensities and satiating capacity (Crum *et al.*, 2011; Deliza & MacFie, 1996; Tijssen *et al.*, 2017).

Although vision was thought to be the dominant means through which we (and our bipedal non-human primate cousins) explore our surroundings (Elliot Smith, 1927; Gilad *et al.*, 2004), a renewed appreciation for the role of olfaction in food search emerged with the finding that humans are able to spatially traverse environments using solely olfactory cues (Porter *et al.*, 2007; Wu *et al.*, 2020; see also Chauvin & Thierry, 2005 and Dominy, 2004 for the integral role of olfaction in primate fruit detection and

selection). These observations are in line with the “olfactory spatial hypothesis”, which contends that the olfactory system of vertebrate species evolved for ecologically-relevant navigational tasks such as locating nearby food sources (Jacobs, 2012). Furthermore, the utility of the olfactory sense for food choice and food intake is well-documented: Odors are majorly responsible for the perception of food flavors (Small & Prescott, 2005), and exposure to ambient odors can trigger an increase in general appetite, as well as appetite specifically for foods with congruent caloric and taste characteristics (so-called “sensory-specific appetite”; Ramaekers *et al.* 2014; Zoon *et al.* 2016). Importantly, these studies collectively demonstrate that odors are able to indirectly communicate a food’s intrinsic nutritional properties prior to ingestion, likely through previous learned pairings between flavors and post-ingestive events (e.g. energy delivery; Yeomans, 2006). However, there is growing evidence that odors can also directly flag the relative fat content – and by proxy energy value – of foods (Boesveldt & Lundstrom, 2014).

Taste is the most “proximal” sense of the three, as it requires immediate contact between a food and the tongue as a basis for either accepting or rejecting a food item (McCrickerd & Forde, 2016). In contrast to vision and olfaction, taste predominantly functions as a macronutrient sensing system and a regulator of food intake *during* food consumption (i.e. via promoting satiation and sensory-specific satiety; Boesveldt & de Graaf, 2017; Vickers *et al.*, 1998). With regards to the former, extensive literature indicates that the two dominant appetitive tastes (i.e. sweet and savory) serve a utilitarian role in the food selection of many species, by signaling the relative nutritional content of ingested resources: Sweet tastes signal a high-sugar (carbohydrate) content, whereas savory (or umami) tastes signal amino acid-rich or protein-rich items (Breslin, 2013; van Langeveld *et al.*, 2017; Teo *et al.*, 2018; Yarmolinsky *et al.*, 2009). Notably, individuals seem to be able to utilize the sense of taste to direct prospective food choice according to internal physiological (homeostatic) needs. For instance, Griffioen-Roose *et al.* (2012) found that protein-deficient individuals displayed a higher preference and oriented choice responses towards savory-tasting (high-protein) foods – the former involving both conscious and subconscious cognitive processes (i.e. increases in implicit and explicit wanting of savory-tasting foods).

1.2.3 Cognitive adaptations for energy-efficient foraging: A high-calorie “bias” in human spatial memory

Although evolved foraging strategies have long been identified in various animal species, ranging from birds (Burke & Fulham, 2003; Cowie, 1977; Sherry *et al.*, 1992; Sulikowski & Burke, 2007) to non-human primates (e.g. Cunningham & Janson, 2007; Janmaat *et al.*, 2014; Janson, 1998), the similar expression of foraging-related cognitive adaptations in humans has received considerably less attention in literature (for some exceptions, see Ferriday *et al.*, 2011; Krasnow *et al.*, 2011; New *et al.*, 2007b). However, in light of the prolonged importance of energy-efficient foraging for the survival and reproduction of ancestral hunter-gatherers (section **1.2.2**), it is reasonable to suspect that our cognitive architecture harbors mechanisms attuned to the efficient procurement of nutritional resources (Nairne & Pandeirada, 2008b; Nairne & Pandeirada, 2010).

Preliminary findings of New *et al.* (2007b) strongly imply the existence of one such foraging-based adaptation in human spatial (location) memory: In an outdoor farmer’s market, participants were led through a randomized route of six food stalls, with each stall featuring a traditionally “gatherable” food resource (e.g. fruits, nuts, or vegetables). Upon arriving at a stall, participants tasted and provided ratings (e.g. taste liking, frequency of consumption) on the food item on offer. Notably, they were unaware that the real aim of the study was to later test their memory for the foods’ locations. After visiting all six stalls, participants were brought to a different area of the market for a “surprise” food spatial memory task, which required them to recall and point to the stall location of each of the six foods in a randomized order. Researchers found that the spatial memory performance of both male and female participants systematically improved (i.e. pointing errors decreased) with a higher caloric density (kcal/100g) of a food, independently of individuals’ explicit effort to remember food locations, or liking and familiarity with an item (see also Seitz *et al.*, 2021 for a recently demonstrated mnemonic effect of caloric content on episodic memory for eating, and Suarez *et al.*, 2019 for a neurobiological basis).

The adaptive significance of an implicit “high-calorie bias” in human spatial cognition can be readily inferred, as it would have optimized habitual foraging efforts by enabling the efficient registration and location of valuable calorie-dense resources – without occupying limited attentional capacities required in other pertinent tasks (e.g.

avoiding predators; Krasnow *et al.*, 2011; New *et al.*, 2007b). Yet given that merely one study has directly alluded to the presence of the cognitive bias so far, more rigorous in-depth examinations of a potential inherent preference in human memory for high-calorie food locations are warranted. For instance, it remains to be elucidated whether the high-calorie spatial memory bias manifests reliably across foraging-relevant sensory modalities (section **1.2.2.1**) and with foods more characteristic of the modern environment, or if the magnitude of the bias' expression varies meaningfully with other individual traits connected to dietary regulation (e.g. External Eating Style; section **1.1**).

1.3. Evolutionarily Mismatched: Foraging Minds in Modern "Obesogenic" Food Environments

1.3.1 Evolutionary mismatch theories of human eating behavior and unhealthy diets

The hypothesis that our physiological and cognitive traits were adaptively selected for during the course of our evolutionary history, and still persist within environments today that are vastly divergent from the ancestral worlds in which they originally evolved, was debuted in the early 1980s (Cordain *et al.*, 2005; Eaton *et al.*, 1988). Since then, "evolutionary mismatch theory" has sparked a wealth of research principally interested in health implications of such discordances, in turn rationalizing health conditions like obesity as a product of a dysfunctional interaction between our selected traits (e.g. preferences for sweet tastes and fatty textures) and certain elements of our current environment (e.g. pronounced availability of ultra-processed energy-dense foods) (Chakravarthy & Booth, 2004; Cordain *et al.*, 2005; Eaton *et al.*, 1988; Li *et al.*, 2017; Lloyd *et al.*, 2011). In support of this narrative, bio-anthropological data convincingly show dietary consequences (e.g. micronutrient deficiencies, increased rates of diabetes and obesity) experienced by foraging communities undergoing a rapid nutrition transition – away from diets dominated by wild (hunted and gathered) resources (see Crittenden & Schnorr, 2016 for a review). The present thesis draws from this evolutionary-informed framework and approaches modern eating behavior specifically from the vantage point of "mismatched" optimal foraging-based mechanisms in human spatial cognition.

1.3.2 Implications of a high-calorie bias in spatial memory for individuals' eating behavior

A second core objective of this thesis was to answer the question of whether (and in what manner) our calorie-sensitive “foraging” minds continue to impinge on our present-day dietary decisions – in environments where the efficient acquisition of foods with high energy-payoffs is no longer a fitness-limiting factor (Brunstrom *et al.*, 2018a; Brunstrom *et al.*, 2018b; Lieberman, 2006). Empirical attempts addressing the latter are lacking, since the study of human cognition in relation to eating behavior has mainly revolved around how episodic “meal” memories or working memory (attentional) faculties moderate prospective food choice and intake (e.g. Robinson *et al.*, 2012; Werthmann *et al.*, 2011; for comprehensive reviews see Higgs, 2016 and Higgs & Spetter, 2018). Also noteworthy is the observation that existing investigations often adopt a traditional (non-functional) viewpoint of memory processes (section **1.2.1**). Namely, manipulations of meal memories are to a large extent assumed to be similarly effective across food products, regardless of possible differences in fitness-related properties (e.g. nutritional quality) between encoded foods. For example, it is thought that rehearsing the hedonic aspects of any recent eating experience can change its remembered enjoyment – and its ensuing effect on future food choice – by uniformly altering consolidation of the meal memory (Robinson *et al.*, 2012; although see Robinson, 2014 for product-specific differences in determinants of remembered enjoyment).

To date, only one study has embodied an adaptive memory perspective and assessed dietary consequences of a suspected high-calorie bias in human spatial cognition: In a controlled-lab experiment, Allan & Allan (2013) examined the association between food location memory and BMI. Using a computer-based spatial memory task, researchers measured individuals' memory for locations of high-calorie snack foods versus that of low-calorie fruits and vegetables. During the experiment, participants judged food stimuli on desirability and rated their current healthy eating intentions. Researchers found that a superior memory for snack food locations – *both* alone and relative to memory for low-calorie food locations – predicted a higher (less healthy) BMI. Importantly, these effects were not attributable to an individuals' food ratings or dietary intentions, as a greater spatial memory accuracy for high- versus low-calorie foods accounted for variance in BMI over and above that by “reflective” psychological

constructs (i.e. rated desirability of snack foods versus fruits and vegetables). This finding led the authors to conjecture that what once was an adaptive feature for promoting positive energy balance in ancestral food-insecure habitats, now poses maladaptive obesogenic consequences for individuals living in urban food-replete environments – especially in those with a marked expression of the cognitive bias.

Yet, mechanistic gaps in knowledge remain. It is presently unclear how exactly a high-calorie bias in spatial memory can give rise to a higher BMI, seeing that the latter represents a very distal indicator of an individual's dietary choices (Bouchard, 2007; Paradis *et al.*, 2009). Reasoning retrospectively, it is conceivable that an improved memory for high-calorie food locations can ultimately contribute to weight gain, by making it easier for individuals to find and subsequently consume energy-dense foods during instances of food decision making (i.e. Allan & Allan, 2013). In other words, a greater expression of the high-calorie spatial memory bias may proximally facilitate high-calorie food search and food choice. Indeed, the convenience or ease of obtaining a food item is an established factor that individuals negotiate, and often favor, in the food choice process (Furst *et al.*, 1996; Sobal *et al.*, 2006). That said, a systematic association with an anthropometric marker of long-term dietary intake also indicates the involvement of more repeated (*routine*) forms of eating behavior. This raises the possibility that the high-calorie spatial memory bias may similarly potentiate unhealthy patterns of behavioral responses (e.g. increased routine frequency of high-calorie food consumption), particularly in light of the fact that single-instance (*incidental*) food choices can create momentum for performing the same behavior within a certain spatiotemporal setting (Furst *et al.*, 1996; Sobal *et al.*, 2006)

In sum, initial evidence suggests that a once functional bias in human spatial memory for high-calorie foods now operates counterproductively to increase individual body weight within a modern food context. The translation of the high-calorie spatial memory bias into suboptimal (long-term) dietary outcomes likely involves (intermediary) effects on both incidental and routine forms of eating behavior (e.g. food search, food choice and consumption). However, the exact behavioral pathways elicited by the cognitive bias – and possible individual-level moderators of these processes (e.g. self-regulation ability; section **1.1**) – require further clarification.

1.4. Aim and Overview of Thesis

The main aim of this thesis was to empirically examine the existence of a potential inbuilt prioritization or “bias” in human spatial memory for high calorie foods, as well as its implications for individual eating behavior within a modern food environment. To this end, we devised the following five studies to systematically address both the *expression* and behavioral *translation* of a high-calorie bias in human spatial memory (see **Table 1.1** and **Figure 1.1** for an overview of central conceptual and methodological aspects of each chapter, as well as the connection between individual thesis chapters):

To establish a proof-of-concept and solid theoretical basis for our remaining studies, we first set out to rigorously investigate whether food-specific biases in human spatial memory are indeed expressed, across sensory modalities (i.e. vision and olfaction) of ecological significance to food navigation and food choice. Therefore, **Chapter 2** reports on two controlled lab experiments featuring a computer-based spatial memory task (Allan & Allan, 2013) with food images (Study 1) and food odors (Study 2), respectively. We also probed associations between food-specific biases in spatial memory and a range of (incidental and routine) eating-related parameters, in order to initially gauge their behavioral effects.

Chapter 3 describes an ambitious test for the existence of the high-calorie spatial memory bias outside of “sanitized” lab settings. To demonstrate the external validity of the bias, we carried out a large multisensory field-based experiment that allowed for two additional noteworthy elements: spatial navigation between distinct (three-dimensional) positions of food stimuli, and the incidental encoding of food locations. This format similarly enabled us to compare food spatial memory performance (and corresponding biases) between different sensory environments (i.e. multisensory versus olfactory conditions).

Chapter 4 improves upon previous lab-based paradigms (cf. **Chapter 2**) to assess the behavioral translation of the high-calorie spatial memory bias, by utilizing a real-world food environment. In a lab-plus-field experiment, we investigated the bias’ effects on the food search and food choice of individuals navigating an unfamiliar supermarket. Across two test sessions, participants first performed eye-tracking and spatial memory tasks in a lab setting, and then completed food search and (covert) food choice tasks in a supermarket.

In **Chapter 5**, our focus was on implications of the high-calorie spatial memory bias for individuals’ *routine* (repeated) eating behavior, to gain insights on top of that provided by more *incidental* (single-instance) measures (cf. **Chapters 2 and 4**). In an online experiment, we examined associations between the cognitive bias and the routine frequency of high-calorie snack consumption, exposure to high-calorie food outlets, and BMI of a large diverse sample of Dutch individuals. For the latter, we assessed individual psychological factors (e.g. snack purchasing habits, inhibitory control) that could either synergize or antagonize the bias’ behavioral effects.

Chapter 6 questions whether the high-calorie bias in spatial memory represents a universal cognitive mechanism and can be reasonably generalized to individuals from varying cultures. Through the means of a cross-cultural online experiment (and data from **Chapter 5**), we measured and compared the food spatial memory of diverse populations from the USA, Japan, and the Netherlands.

Finally in **Chapter 7**, we reflect on our main findings and their practical utility for the promotion of healthy eating, discuss the methodological composition of this thesis, and identify exciting directions for future research.

Table 1.1. An overview of the primary research objectives of each thesis chapter.

Chapter	Primary Research Objectives
2	Investigate the existence of a high-calorie bias in human spatial memory across foraging-relevant sensory modalities, and its effects on (incidental and routine) eating behavior
3	Investigate the existence of a high-calorie bias in human spatial memory within a naturalistic (three-dimensional) multisensory food environment
4	Investigate effects of the high-calorie spatial memory bias on the food search and food choice of individuals navigating a real-world food environment
5	Investigate effects of the high-calorie spatial memory bias on individuals’ routine eating behavior, across diverse sociodemographic groups within a (Dutch) population
6	Investigate the generalizability of the high-calorie bias in human spatial memory across diverse cultures, as well as sociodemographic groups within (US and Japanese) populations

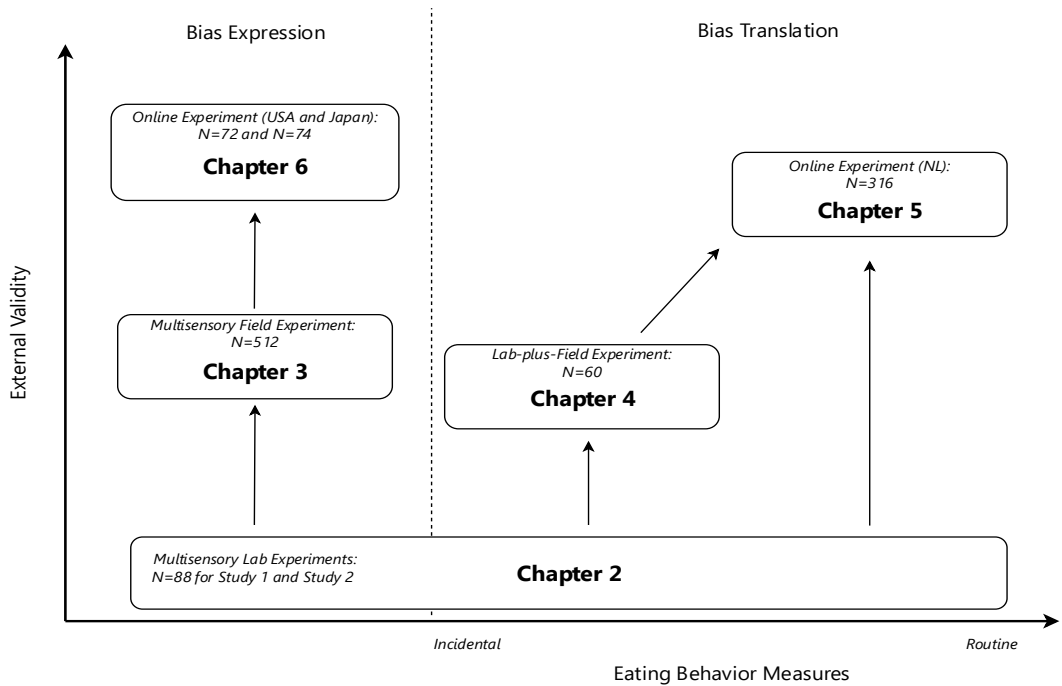
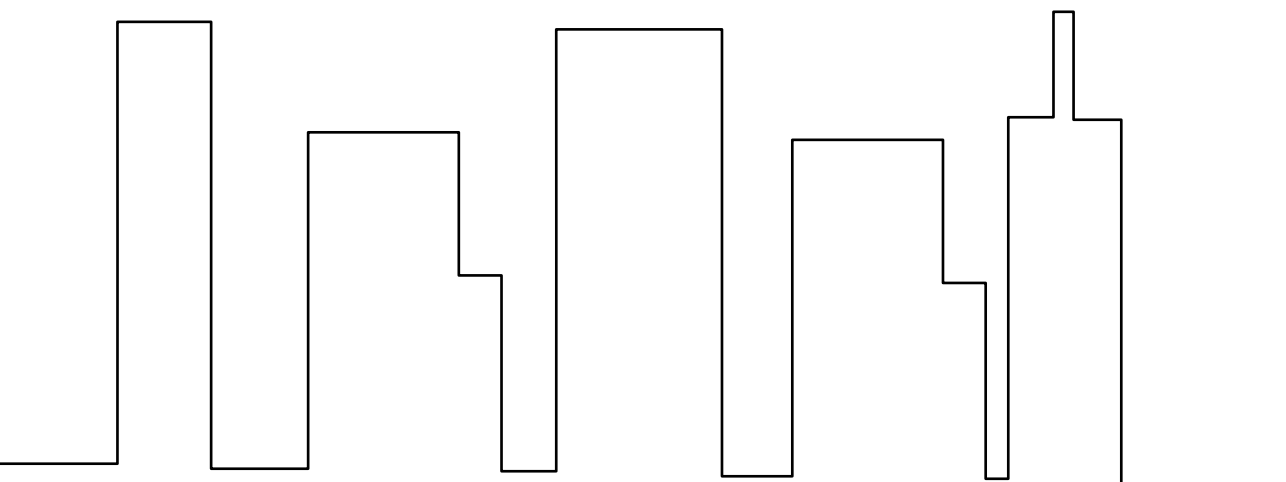


Figure 1.1. An illustration of the central conceptual (i.e. bias expression versus bias translation) and methodological aspects of each thesis chapter, and the relation between different chapters. Boldened arrows indicate the direction in which results of one chapter directly informed central research questions of the other.



Rachelle de Vries

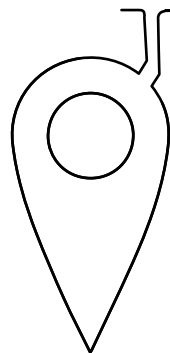
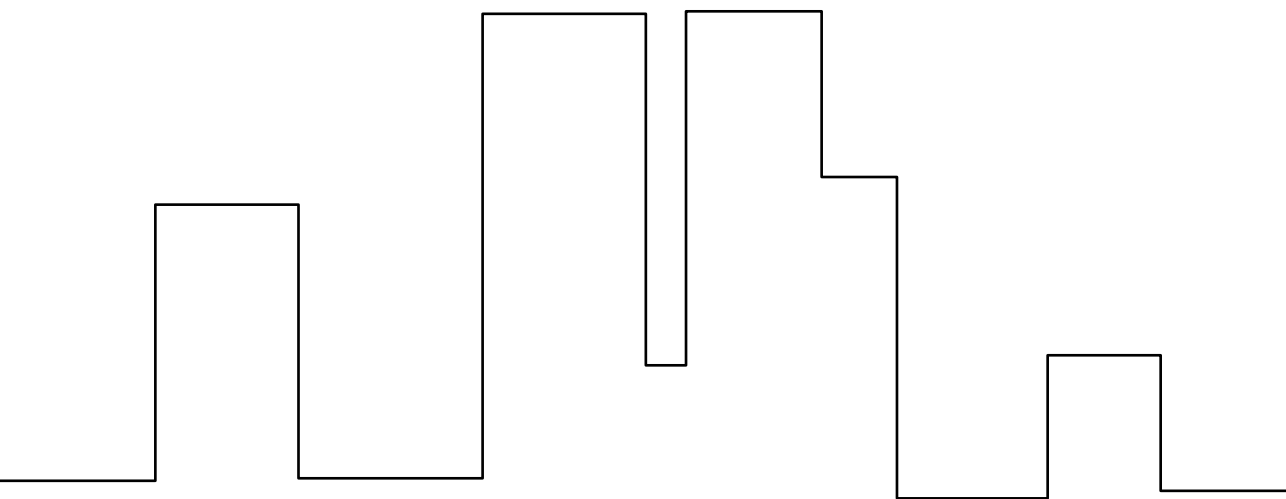
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Chapter 2

Foraging minds in
modern environments:
High-calorie and savory-taste
biases in human food spatial
memory

Abstract

Human memory may show sensitivity to content that carried fitness-relevance throughout evolutionary history. We investigated whether biases in human food spatial memory exist and influence the eating behavior of individuals within the modern food environment. In two lab studies with distinct samples of 88 participants, individuals had to re-locate foods on a map in a computer-based spatial memory task using visual (Study 1) or olfactory (Study 2) cues that signaled sweet and savory high- and low-calorie foods. Individuals consistently displayed an enhanced memory for locations of high-calorie and savory-tasting foods – regardless of hedonic evaluations, personal experiences with foods, or the time taken to encode food locations. However, we did not find any clear effects of the high-calorie or savory-taste bias in food spatial memory on eating behavior. Findings highlight that content matters deeply for the faculty of human food spatial memory and indicate an implicit cognitive system presumably attuned to ancestral priorities of optimal foraging.

General Introduction

The prevailing view in cognitive psychology assumes that human memory consists largely of domain-general mechanisms that are insensitive to the content which is processed (Tulving & Thomson, 1973). Conversely, advocates of a more functionalist agenda of human cognition contend that much like other biological systems, memory and its operational systems did not evolve in a vacuum (Nairne & Pandeirada, 2008b). Rather, memory faculties were subject to the constraints of nature's criteria and thus should be functionally designed to preferentially process fitness-relevant information and solve adaptive problems (Nairne & Pandeirada, 2010). One such adaptive problem encountered across species is the efficient location and acquisition of nutritional resources (Schoener, 1971). This research entertains the notion that natural selection processes shaped a cognitive adaptation that enabled ancestral humans to thrive within erratic food habitats of the past – a bias in spatial memory for high-calorie foods.

During the substantial majority of human evolution, hunter-gatherers needed to forage intensively to attain sufficient nutrition (Eaton, 2006). Survival was thus contingent upon an individual's ability to efficiently identify and gather high-quality resources within a complex and variable physical environment, as well as to retrace those resources as they became valuable over time, by using input from various sensory modalities (New *et al.*, 2007b; Winterhalder, 1981). As a result, natural selection pressures might have favored a functional 'bias' in spatial processing that enables the effortless registration and memory of locations of valuable calorie-dense foods (Krasnow *et al.*, 2011; New *et al.*, 2007b). Such an inbuilt spatial processing bias entails a preference in location memory for high-calorie foods, irrespective of individual hedonic evaluations or personal experiences. It follows that a once adaptive spatial memory mechanism could yield adverse obesogenic effects for individuals with a greater expression of the bias in present-day food-replete settings, by enhancing the navigational ease through which unhealthy high-calorie items are obtained and subsequently consumed (Allan & Allan, 2013). However, literature on a potential high-calorie bias in spatial memory – and its implications for food choice and dietary intake within a modern food context – remains relatively nascent. Only two pieces of evidence have accumulated so far: New and colleagues (2007b) were the first to discover that a food's caloric content positively predicted the accuracy with which (blinded) individuals pointed to previously visited vendor locations within an outdoor farmers' market.

Subsequently, Allan & Allan (2013) found that an improved spatial memory for high-calorie snacks (versus low-calorie fruits and vegetables) was associated with a higher BMI in women, although they did not explicitly test the existence of the high-calorie spatial memory bias itself. Therefore, the present paper represents the first to systematically investigate the expression and potential behavioral effects of food-specific biases in human spatial memory under rigorous lab conditions.

It is similarly unknown what food- or person-specific characteristics are associated with this cognitive bias. Optimal foraging models of evolutionary ecology posit taste to be one such food-related factor. Taste perception is thought to bear great relevance to the course of hominid evolution, with sweet and savory (i.e. umami) representing the two dominant 'appetitive' taste modalities across many species (Breslin, 2013; Yarmolinsky, Zuker, & Ryba, 2009). Namely, tastes are thought to have aided hunter-gatherers in productive food selection by signaling specific nutritional contents of consumed resources – sweet for the presence of (energy-rich) sugars and carbohydrates, and savory for amino-acid or protein content (Breslin, 2013; Teo *et al.*, 2018; Yarmolinsky *et al.*, 2009, although see Langeveld *et al.*, 2017 and Lease, Hendrie, Poelman, Delahunty, & Cox, 2016 for discussion on the relationship between sweet taste and energy content). As sweet- and savory-tasting foods (e.g. fruit versus meat) serve distinct functional roles and varying priorities were potentially placed on energy versus nutrient (protein) intake during foraging, differences in spatial memory adaptations may have manifested between the respective taste modalities and their associated foods (Eaton, 2006).

The magnitude of the high-calorie bias in food spatial memory may also vary meaningfully with person-specific characteristics such as (trait) eating styles or reward sensitivity. Within an evolutionary context, a high reactivity to external (rewarding) cues is assumed to have carried a survival advantage under conditions of resource constraint (Lieberman, 2006; Ulijaszek, 2002). Based on empirical observations, individual propensities for restrained eating, external eating, as well as sensitivity to rewarding stimuli, facilitate overeating through pathways such as disruptions in self-control and are positively associated with BMI (Castellanos *et al.*, 2009; Davis *et al.*, 2007; van Strien *et al.*, 1986). In a similar vein, restrained eaters, external eaters, and those high in reward sensitivity are documented to exhibit marked attentional biases towards high-calorie food stimuli (Hou *et al.*, 2011; Meule *et al.*, 2012b; Tapper *et al.*, 2010). However,

whether any of the former outcomes are systematically associated with a high-calorie bias in spatial memory has not been investigated to date and merits further exploration.

The aim of the present research was two-fold: In two lab studies, we sought to demonstrate the existence of a high-calorie bias in human food spatial memory and its consequent effects on eating behavior and objective long-term markers of dietary intake. As a secondary objective, we explored potential food (i.e. Taste) and person-specific factors (i.e. Eating Styles and Reward Sensitivity) associated with an enhanced location memory for high-calorie foods. To this end, a computerized food spatial memory paradigm was used with varying caloric density (High versus Low) and taste (Sweet versus Savory) conditions. Two classes of sensory food stimuli with evolutionary significance to the process of food navigation were used in the experimental paradigm: visual (Study 1) and olfactory (Study 2) food cues.

In line with previous findings, the following outcomes were hypothesized:

H_{1A} : Individuals display a greater overall accuracy in spatial memory for high-calorie foods compared to low-calorie alternatives – regardless of hedonic evaluations or familiarity with foods.

H_{1B} : The high-calorie bias in spatial memory predicts unhealthy eating behaviors (e.g. food choice) and higher anthropometric markers of dietary intake (e.g. BMI).

H_2 : Taste and person-specific factors interact with the caloric density of foods, such that sweet and savory high-calorie food locations are differentially retained, and an enhanced reward sensitivity – as well as restrained and external eating tendency – confers a larger degree of bias expression.

Study 1

Methodology

Participants

A total of 88 healthy university students (68% female; $M_{\text{Age}} = 24.7$ years, $SD = 2.7$, range 18-35 years) from various ethnic (65% Caucasian; 23% Asian; 9% Latino; 3% African and Arab) and educational backgrounds (76% postgraduates; 24% undergraduates) took part in the research. The sample size was determined by *a priori* power calculations: On the basis of previous work (Allan & Allan, 2013; New *et al.*, 2007b), we estimated an effect size f^2 of 0.14 and power of 0.80 for the association

between the high-calorie spatial memory bias and BMI (as a proxy for long-term dietary intake). The final sample size would also allow us to systematically adjust for any order effects, by ensuring that an equal number of individuals were assigned to the different treatment orders. Participants were limited to the BMI range of 18.5 – 30 kg/m² ($M = 22.5$ kg/m², $SD = 2.2$), to control for differential cognitive processing of food stimuli in extreme (i.e. underweight < 18.5 kg/m² and obese > 30 kg/m²) weight classes (Castellanos *et al.*, 2009; Giel *et al.*, 2011). Furthermore, individuals did not take part in the study when reporting a psychological or physical intolerance to tested foods (e.g. meat), or in case of a (self-reported) medical history of eating or psychiatric disorders. Recruitment was achieved through the advertisement of study posters and flyers on campus buildings, social media platforms, and participant mailing lists. After providing written informed consent and completing two test sessions, participants were compensated with a 10 euro giftcard. This study received ethical approval from the Social Sciences Ethics Committee of Wageningen University, and was preregistered on the Open Science Framework database (Project URL: osf.io/ufrqv).

Design

The current study had a 2 (Caloric Density: High versus Low) by 2 (Taste: Sweet versus Savory) within-subjects crossover design. Participants were randomly assigned to complete four caloric density - taste conditions (High-Sweet [H_SW] e.g. Chocolate; High-Savory [H_SA] e.g. Chips; Low-Sweet [L_SW] e.g. Fruit; Low-Savory [L_SA] e.g. Vegetables) in two successive test sessions separated by a washout period of (at least) one week. Within a test session, each participant was required to perform a spatial memory task for two conditions. Importantly, the final randomization of orders was balanced; an equal number of individuals began in each caloric density - taste condition.

Apparatus and Stimuli

Spatial memory task. The original E-Prime scripts and university campus setting of Allan & Allan (2013) were used to test food spatial memory. Participants were asked to imagine that an international food market – encompassing 24 food stalls – was taking place on a (unfamiliar) university campus. Depending on the treatment condition, participants were then shown a sequence of 12 pictures of either (sweet/savory) high-calorie items or low-calorie alternatives, followed by an image of a university campus map showcasing all possible stall locations ($N=24$), at a fixed duration

of three seconds each. Next, the locations of the stalls selling each food item (N=12) were sequentially indicated on the campus map by a green crosshair. During the location viewing process, participants were instructed to rate each food item on desirability and familiarity, and this was done at a self-determined pace. Following a two-minute break, participants were exposed to a series of 12 spatial memory tests in which they were randomly presented with one of the previously shown food images and required to specify (via mouse-click) its correct corresponding stall location on the campus map. The total number of possible stall sites (N= 24) was displayed for the spatial memory tests, and a stall location could be selected more than once. Assigned stall locations did not overlap for foods within a test session.

Stimulus presentation. The psychology software tool E-prime (version 2.0) was used for stimulus presentation and subsequent spatial memory tasks. Computers were standardized across the parameters of screen size (*15.6 inches*), resolution (*1920 x 1080*), and refresh rate (*60 Hertz*). The order of stimulus presentation and the stimuli itself (i.e. food-location pairs within a campus map) were randomized differently for each participant.

Food images. Images of (sweet/savory) high- and low- calorie foods were obtained from the *Food Pics* database, where available pictures are homogenous with respect to resolution (*600 x 450 pixels*), color depth (*96 dpi*), background color (*white*), and camera distance (*~80 cm*) (Blechert *et al.*, 2014). A set of 12 (unbranded) food pictures was selected to represent each caloric density - taste category – encompassing fruits and vegetables for the low-calorie condition, and baked and fried goods as high-calorie variants (**Figure 2.1**). High-calorie items were defined as those that contained at least 225 – and low-calorie items at most 60 – kcal per 100 grams of food (de Bruijn *et al.*, 2017; World Cancer Research Fund/American Institute for Cancer Research, 2007). Chosen food stimuli (N=48; see *Food Pics* Catalogue Numbers in the Supplemental Material (**Appendix Chapter 2**)) were matched on recognizability and subjective palatability across caloric density and taste groups using metadata from the *Food Pics* database [all p s >.05], and additionally piloted in a separate sample of students (N= 32, 53% female; M_{Age} = 23.6 years, SD = 2.75) to ensure consistencies in caloric content, taste, and healthiness perceptions (see Supplementary Material for the pilot questionnaire (**Appendix Chapter 2**)).

The final selection of high-calorie images displayed a significantly greater mean caloric density (High-calorie: $M = 368.40$ kcal/100g, $SD = 108.40$; Low-calorie: $M = 30.21$ kcal/100g, $SD = 16.61$), $t(24) = 15.11$, $p < .001$, as well as total energy content (High-calorie: $M = 638.37$ kcal/image, $SD = 731.72$; Low-calorie: $M = 135.96$ kcal/image, $SD = 234.84$), $U = 72.00$, $p < .001$, compared to the low-calorie group. High-calorie images were also perceived as higher in caloric content (High-calorie: $M = 76.44$ mm, $SD = 14.92$; Low-calorie: $M = 24.40$ mm, $SD = 17.45$), $Z = -11.63$, $p < .001$, and less healthy (High-calorie: $M = 24.24$ mm, $SD = 19.30$; Low-calorie: $M = 77.53$ mm, $SD = 15.92$), $Z = -11.36$, $p < .001$, than low-calorie images. Likewise, sweet pictures scored higher on sweet taste expectations (Sweet: $M = 74.87$ mm, $SD = 17.29$; Savory: $M = 24.05$ mm, $SD = 20.60$), $Z = -11.45$, $p < .001$, and savory pictures were valued greater on expected savoriness (Savory: $M = 58.20$ mm, $SD = 25.00$; Sweet: $M = 34.27$ mm, $SD = 29.95$), $Z = -7.29$, $p < .001$.

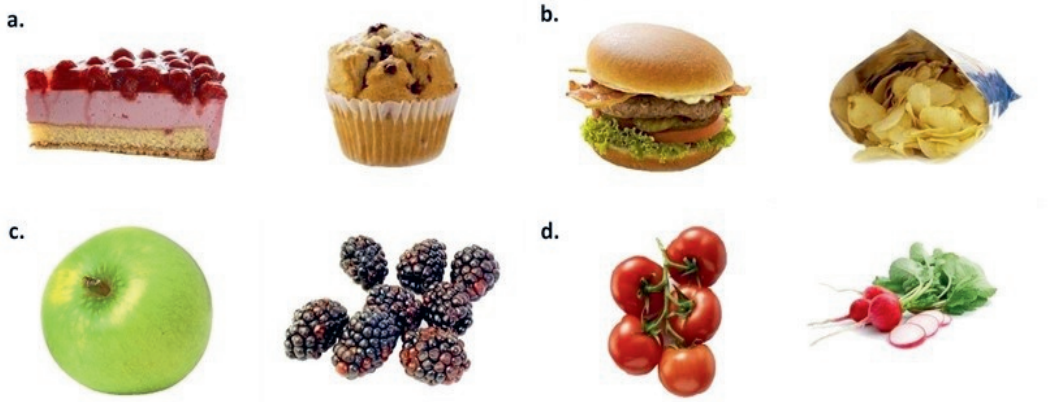


Figure 2.1. Selection of food images from the *Food Pics* database (Blechert *et al.*, 2014). Examples of (a) high-sweet, (b) high-savory, (c) low-sweet, and (d) low-savory items.

Procedure

Prior to starting, participants were informed that the experiment aimed to investigate individuals' memory for specific foods. The spatial faculty of memory was intentionally not emphasized to diffuse suspicions on the true aim of the study, and post-hoc (open-ended funneling) debriefing interviews confirmed the efficacy of the cover story. Participants were also informed that good performance would earn them a prize at the end of the experiment, in an effort to disguise our (covert) food choice measure and motivate participants to complete tasks as accurately as possible. Hunger

states were standardized before testing by instructing individuals to consume their habitual meals or snacks no later than two hours – and no sooner than 45 minutes – before test sessions, during which only water intake was permitted.

Upon arrival, participants' height and weight were recorded. After, participants were directed to and seated in isolated testing booths fitted with a laptop. Demographics (e.g. subjective SES), hunger state, restrained eating, external eating, and reward sensitivity data were first collected via a questionnaire. Individuals then had to perform a series of computer-based spatial memory tasks (adapted from Allan & Allan (2013), see detailed explanation above): A practice trial that involved the encoding and recall of (non-food) object locations was first carried out, to familiarize participants with the spatial memory task. Participants then proceeded to complete the actual spatial memory task with food images from the first caloric density- taste condition. After finishing, they evaluated their (perceived) performance on the preceding task. Following a brief (five minute) intermission, the protocol was repeated for the other assigned caloric density - taste condition. A test session lasted, on average, 40 minutes.

After participants completed the study procedure for the remaining two caloric density- taste conditions approximately one week later in the second test session, they answered questions about healthy eating goals. Regardless of performance, participants were then led individually to a cubicle and presented with a preselected array of foods. Individuals were instructed to choose one food as their prize for performing and were left alone to make their decision. Results of the covert food choice task were noted down by the experimenter.

Measurements

Primary outcome variables. *Spatial memory accuracy* for (sweet/savory) high- and low-calorie foods was tabulated as the average 'pointing error' or Euclidian distance (D) between true and indicated stall locations of each food type (cf. Allan & Allan, 2013; Nairne *et al.*, 2012). Consequently, lower D scores denote a higher accuracy in food spatial memory. *Spatial memory bias* for (sweet/savory) high-calorie foods was operationalized as the discrepancy in spatial memory accuracy between high- versus low-calorie foods ($D_{\text{High Calorie}} - D_{\text{Low Calorie}}$) (cf. Allan & Allan, 2013). Accordingly, negative values indicate an enhanced spatial memory for calorie dense foods.

Secondary outcome variables. *Food choice* was assessed through the means of a covert forced-choice task, as a first step in exploring whether effects on relevant

proximal aspects of eating behavior could manifest. A selection of foods comprising the previously tested caloric density - taste groups (H_SW: Chocolate bars; H_SA: Chips; L_SW: Apples; L_SA: snack tomatoes) was placed in wooden baskets and presented to participants individually at the conclusion of testing as a reward. Foods on offer represented small 'snack' items and were deemed appropriate within a university and day setting to control for possible contextual effects on choice. Moreover, locations of food groups within the baskets were randomized in each test session to rule out accessibility or convenience issues.

In addition, height (m) and weight (kg) measures were collected with an electronic scale (SECA 704) and stadiometer (SECA 213) to obtain accurate $BMI(kg/m^2)$ values.

Predictor variables. Individual predispositions for *Restrained* and *External Eating* were quantified through averaging associated subscales of the Dutch Eating Behavior Questionnaire (Cronbach's $\alpha = .86$ and $.86$, respectively) (van Strien *et al.*, 1986). Higher scores, from a possible range of 1 to 5, point at greater tendencies towards respective eating styles.

Furthermore, the Behavioral Activation System (BAS) scale was used to gauge individuals' degree of *Reward Sensitivity* (Carver & White, 1994). Scores range from 1 to 4 for all three BAS-related subscales (Reward Responsiveness; Drive; Fun Seeking), with lower values denoting greater behavioral activation sensitivities to rewarding stimuli. As two BAS subscales proved to have poor internal consistencies in our sample (Cronbach's $\alpha \leq .68$), scores of the three subscales were aggregated in order to form a more reliable total BAS measure (Cronbach's $\alpha = .79$). In doing so, the number of parameters to be estimated in statistical models was also favorably reduced relative to our sample size.

Control measures. To account for extraneous effects of 'wanting' of food types on spatial memory accuracy, we instructed participants to rate each item's *Desirability* by indicating on a 100mm VAS (anchored from "Not At All" to "Very Much") their desire to eat the displayed food item (see Food Stimuli Ratings in the Supplemental Material (**Appendix Chapter 2**)). In addition, effects of individual exposure to a food type were controlled through the use of a five-item *Familiarity* scale (Tuorila *et al.*, 2001). Two socioeconomic indexes – postal codes and the 10-point MacArthur Subjective Social Status Scale – were also recorded owing to the respective relationships of

suboptimal dietary patterns with low neighborhood and (subjective) individual SES (Goodman *et al.*, 2001; Lakerveld *et al.*, 2015). For the former, postal codes were transformed into z-distributed scores of neighborhood SES using information from the *Statusscores* database of the Netherlands Institute for Social Research (SCP Statusscores, 2017).

As dietary behaviors and BMI may likewise be contingent upon the strength of an individual's explicit nutritional intentions, a *Healthy Eating Goals* measure was administered with two items (*In my daily life, I strive to eat healthy, It is important to me to eat healthy foods*) rated on a seven-point scale anchored from "Strongly Disagree" to "Strongly Agree" (Raghoebar, van Kleef, de Vet, *under review*). *Perceived Performance* was additionally measured on a 100mm VAS (anchored from "Not Good At All" to "Very Good"), as proxy of awareness of the bias. Finally, a general questionnaire documented both pertinent demographic characteristics (e.g. *Sex, Age, Ethnicity*) and *Hunger* states (100mm VAS anchored from "Not At All" to "Very Much") at encoding.

Data Analysis

Data were analyzed using IBM SPSS Statistics 23 with statistical significance defined as $p < .05$. A linear mixed effects model was chosen to analyze food spatial memory data, as it represents a flexible and robust manner of modelling continuous outcomes when the assumption of independent errors is relaxed (Krueger & Tian, 2004). With regards to linear mixed effects modelling, a backward elimination approach was adopted for model selection, given that it is less prone to underfitting data and yielding biased (fixed effect) estimates (Cheng *et al.*, 2009). First, the covariance structure of saturated models (see below) was determined based on Restricted Maximum Likelihood (REML) likelihood ratio tests using the -2 log likelihood (-2LL) test statistic; fixed effects were subsequently finalized based on Maximum Likelihood (ML) ordinary likelihood ratio tests using the -2LL test statistic. In either case, a selection was made on the basis of parsimony and final models were refitted with REML estimations. Hypotheses and corresponding statistical analyses were registered prior to observing data. Slightly deviating from our pre-registration form, *perceived performance* ratings were correlated with actual spatial memory performance and compared between caloric density - taste conditions.

Caloric density, taste, person-specific factors, and food spatial memory accuracy (H_{1A} and H₂). To determine whether the accuracy of food spatial

memory varies meaningfully with caloric content or taste aspects, we formulated a random intercept and slope linear mixed model with main and interaction effects of *Caloric Density* and *Taste* as fixed factors, *Participant* and *Test Session* as random factors (covariance structure: Unstructured), *Sex*, *Age*, *Ethnicity*, *Neighborhood SES*, *Subjective SES*, *Taste Order*, *Desirability*, *Familiarity*, and averaged *Hunger* scores as covariates, and *Spatial Memory Accuracy* (D) as the dependent variable.

To examine person-specific factors that could predict the magnitude of food spatial memory accuracy, we included main and interaction effects (with *Caloric Density*) of *Restrained Eating*, *External Eating*, and *Reward Sensitivity* as predictor variables.

Spatial memory bias for high-calorie foods and food choice (H_{1B}). To ascertain the effects of a high-calorie bias in spatial memory on eating behavior, we conducted a binomial logistic regression ($N=1$; simultaneous entry method) with the log odds ratio of *High-Calorie Food Choice* as the dependent variable and *Sex*, *Age*, *Ethnicity*, *Neighborhood SES*, *Subjective SES*, *Restrained Eating*, *External Eating*, *Reward Sensitivity*, *Desirability* of High- and Low-calorie foods, *Familiarity* with High- and Low-calorie foods, *Hunger* ratings of the final test session, *Healthy Eating Goals* and *Spatial Memory Bias* for High- versus Low-calorie foods ($D_{\text{High Calorie}} - D_{\text{Low Calorie}}$) as predictor factors.

Spatial memory bias for high-calorie foods and BMI (H_{1B}). A multiple linear regression ($N=1$; simultaneous entry method) was performed on *BMI*, with *Sex*, *Age*, *Ethnicity*, *Neighborhood SES*, *Subjective SES*, *Restrained Eating*, *External Eating*, *Reward Sensitivity*, *Desirability* of High- and Low-calorie foods, *Familiarity* with High- and Low-calorie foods, *Healthy Eating Goals*, and *Spatial Memory Accuracy* of respective food groups ($D_{\text{High Calorie}}$ and $D_{\text{Low Calorie}}$) as predictors, to test whether food spatial memory would account for variation in long-term markers of dietary intake.

A final multiple linear regression model ($N=1$; simultaneous entry method) was formulated to determine the relative effects of high- and low-calorie food spatial memory on BMI. Accordingly, *Sex*, *Age*, *Ethnicity*, *Neighborhood SES*, *Subjective SES*, *Restrained Eating*, *External Eating*, *Reward Sensitivity*, *Desirability* of High- versus Low-calorie foods, *Familiarity* with High- versus Low-calorie foods, *Healthy Eating Goals*, and *Spatial Memory Bias* for High- versus Low-calorie foods ($D_{\text{High Calorie}} - D_{\text{Low Calorie}}$) were entered as independent variables.

Results

Food Spatial Memory: Accuracy and Biases

The average pointing error in food spatial memory across all caloric density-taste conditions amounted to 129.71 pixels (95% CI = [124.09,135.32]). Perceived performance ratings mirrored actual spatial memory performance (i.e. pointing errors) moderately well ($r_s(350) = -.66; p < .001$). Perceived performance did not differ between caloric density (*Mean difference*_{High-Low calorie} = 2.44 mm, 95% CI = [-1.05,5.93]), $t(87) = 1.39, p = .169, d = 0.15$, or taste conditions (*Mean difference*_{Sweet-Savory} = -2.99 mm, 95% CI = [-7.38,1.39]), $t(87) = -1.36, p = .179, d = 0.14$.

Individuals displayed an overall enhanced memory for the location of high-calorie foods (i.e. smaller pointing error or D) relative to low-calorie counterparts, $F(1,4049) = 8.25, p = .004, \eta^2 = 0.002, 90\% \text{ CI } \eta^2 [0.0004, 0.005]$, indicating a bias in spatial memory in favor of high-calorie foods (**Figure 2.2**). Similarly, a main effect of Taste was shown with savory food locations more accurately recalled than sweet alternatives, $F(1,4063) = 36.35, p < .001, \eta^2 = 0.009, 90\% \text{ CI } \eta^2 [0.005, 0.01]$, suggesting the further presence of a savory-taste bias in food spatial memory. These bias effects persisted regardless of demographics (e.g. Sex), hedonic evaluations, or personal familiarity with respective foods. Controlling for the time participants spent rating foods and encoding corresponding locations only marginally attenuated Caloric Density effects on food spatial memory accuracy, $F(1,4047) = 5.46, p = .019$, and exerted no influence on Taste effects, $F(1,4064) = 29.04, p < .001$. The time participants took to recall food locations did not have an effect on spatial memory performance, $F(1,84) = 0.17, p = .679, \eta^2 = 0.002, 90\% \text{ CI } \eta^2 [0, 0.04]$.

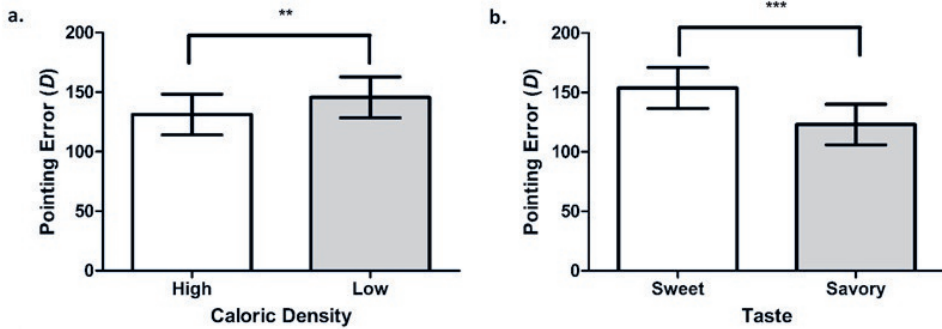


Figure 2.2. Spatial memory for (a) Caloric Density and (b) Taste food groups. Spatial memory accuracy was operationalized as the “pointing error” or distance in pixels (D) between true and indicated food locations, with lower D values denoting a higher accuracy in food spatial memory. A double asterisk indicates a significant difference with a p value lower than .01 and a triple asterisk indicates a significant difference with a p value lower than .001. Error bars represent 95% confidence intervals.

Taste and Person-specific Moderators

The effect of Caloric Density on food spatial memory accuracy was not moderated by the Taste of a food, $F(1,86.14) = 0.88$, $p = .352$, $\eta^2 = 0.01$, 90% CI $\eta^2 [0, 0.07]$. Likewise, none of the included person-specific factors (i.e. Restrained Eating, External Eating, Reward Sensitivity) and associated interactions (with Caloric Density) predicted spatial memory performance (all $p > .05$, $\eta^2 = 0.001 [0, 0.003]$, $3 \times 10^{-6} [0, 3 \times 10^{-4}]$, and $1 \times 10^{-4} [0, 0.001]$, respectively).

Food Choice

Contrary to expectations, the high-calorie bias in spatial memory was not predictive of prospective high-calorie food choice (OR = 1.00, 95% CI = [0.99, 1.01]), Wald statistic (1) = 0.01, $p = .925$. Rather, an individual’s reported healthy eating intentions negatively predicted the odds of choosing a high-calorie food reward (OR = 0.49, 95% CI = [0.24, 0.97]), Wald statistic (1) = 4.17, $p = .041$. A corresponding analysis was conducted to explore the influence of the savory-taste bias in spatial memory on savory food choice. Similarly, the bias in spatial memory for savory-tasting foods was not associated with the odds of choosing a savory reward (OR = 1.01, 95% CI = [1.00, 1.01]), Wald statistic (1) = 2.47, $p = .116$.

Spatial Memory Bias for High-calorie Foods in relation to BMI

BMI was not significantly associated with either spatial memory for high- ($B = -0.004$, 95% CI = [-0.01, 0.002]), $t(72) = -1.31$, $p = .194$, or low-calorie food items ($B = .002$, 95% CI = [-0.004, 0.01]), $t(72) = 0.64$, $p = .527$. Taking into account the relative

difference in high- versus low-calorie food spatial memory (i.e. the high-calorie spatial memory bias), the high-calorie bias in spatial memory was likewise not predictive of BMI ($B = -0.003$, 95% CI = $[-0.01, 0.002]$), $t(75) = -1.18$, $p = .122$. Conversely, an individual's Healthy Eating Goals, Sex, and Desirability (bias) for high-calorie foods were significant correlates across statistical models (see **Table A2.1** in the Supplemental Material for the complete statistical output).

Interim Discussion

Using visual food cues in a controlled lab setting, results show that individuals displayed a more accurate memory for high-calorie food locations relative to low-calorie counterparts. Interestingly, a main effect of taste was found, as individuals also better remembered locations of savory- as opposed to sweet-tasting foods. These effects were not explicated by differences in hedonic evaluations of foods, personal familiarity with foods, or the (objective) time taken to encode and recall food locations. The magnitude of the high-calorie bias was not further moderated by eating style tendencies or reward sensitivity. Finally, the high-calorie spatial memory bias elicited small and non-significant changes in prospective food choice and BMI, whereas an individual's healthy eating goals was largely associated with both a lower likelihood of high-calorie food choice and BMI.

Given that olfaction is an evolutionary old (anticipatory) sense that is intrinsically linked to spatial memory and food decision making (Boesveldt & de Graaf, 2017; Dahmani *et al.*, 2018), Study 2 investigated whether biases in food spatial memory would likewise manifest with odors signaling (sweet/savory) high- and low-calorie food items. The sense of smell is important across foraging species for navigational tasks such as locating food sources, and the ability of humans to utilize odor information as spatial cues appears to be intact (Jacobs, 2012; Schifferstein *et al.*, 2009). Moreover, in light of the fact that the previous food choice measure encompassed a limited variety of foods and "reward" connotations may have influenced decision making, Study 2 explored potential effects of biases in food spatial memory on a wider spectrum of eating-related outcomes. We included a validated measure of food preference – an established psychological determinant of food choice – which reliably predicts individual preference for a large assortment of (sweet/savory) high- and low-calorie products (de Bruijn *et al.*, 2017; Furst *et al.*, 1996; Yeomans, 2006). Finally, in addition to BMI, we collected data on waist circumference, as it has been shown to be a more sensitive

anthropometric marker of (abdominal) adiposity that is less susceptible to confounding by muscle mass (Stevens *et al.*, 2008).

Study 2

Methodology

Participants

A total of 88 healthy Dutch university students (78% female; $M_{\text{Age}} = 21.9$ years, $SD = 2.0$, range 18-35 years; $M_{\text{BMI}} = 20.6 \text{ kg/m}^2$, $SD = 0.8$) from various educational backgrounds (48% postgraduates; 52% undergraduates) took part in the research. The sample size was chosen to remain consistent with that of Study 1, as spatial memory performance for vision and olfaction were expected to be similar (Schifferstein *et al.*, 2009). Participants were limited to Dutch individuals given the use of culture-specific task stimuli. All other inclusion and exclusion criteria as stipulated for Study 1 were applied. Furthermore, participants were screened for a normal olfactory sense (scoring $\geq 75\%$ correct on the 16-item Sniffin' Sticks identification test) and the absence of habitual smoking (Katotomichelakis *et al.*, 2007; Kobal *et al.*, 1996). Individuals that participated in the former study, reported a history of neurological or olfactory disorders, or were pregnant and/or lactating were not included (Ochsenbein-Kölble *et al.*, 2007). Recruitment was achieved through the advertisement of study posters and flyers on campus buildings, social media platforms, and participant mailing lists. After providing written informed consent and completing a screening session in addition to two test sessions, participants were compensated with a 25 euro giftcard. This study received ethical approval from the Social Sciences Ethics Committee of Wageningen University, and was preregistered on the Open Science Framework database (Project URL: osf.io/8u2xa).

Design

Paralleling Study 1, the current study had a 2 (Caloric Density: High versus Low) by 2 (Taste: Sweet versus Savory) within-subjects crossover design with a washout period of (at least) one week.

Apparatus and Stimuli

Spatial memory task. The original E-Prime scripts and university campus setting of Allan & Allan (2013) were used to test food spatial memory. Participants were

asked to imagine that an international food market – encompassing 12 food stalls – was taking place on a (unfamiliar) university campus. Depending on the treatment condition, participants were then asked to smell four (sequential) odor solutions that signaled either (sweet/savory) high-calorie foods or low-calorie alternatives at a fixed duration of five seconds each (Brünner *et al.*, 2015). During the smelling of a food odor, the location of the stall selling the corresponding food item was displayed on the university campus map through the means of a green crosshair. Between presentations of odor-location pairs, individuals rested for an interval of 20 seconds and smelled the inner portion of their wrist in order to avoid olfactory fatigue and odor carry-over effects (Brünner *et al.*, 2015). Following a two-minute break after the presentation of the last odor-location pair, participants were exposed to a series of four spatial memory tests in which they were randomly presented with one of the previous food odors and required to specify (via mouse-click) its correct corresponding stall location on the campus map. Similarly, individuals rested for an interval of five seconds and smelled their inner wrist between odor-location recalls. The total number of possible stall sites ($N=12$) was displayed for the spatial memory tests, and a stall location could be selected more than once. Assigned stall locations did not overlap for food odors within a test session.

The spatial memory task was piloted beforehand to match difficulty levels as closely as possible with that of Study 1. Although the odor-based spatial memory task encompassed a lower number of food locations to encode and recall, it was not inherently easier to perform (Mean pointing error Study 2 = 196.11 pixels, $SD = 206.05$; Mean pointing error Study 1 = 129.71 pixels, $SD = 186.11$), $U = 116147.00$, $p = .003$, $d = 0.34$.

Stimulus presentation. The psychology software tool E-prime (version 2.0) was used for spatial memory tasks. Computers were standardized across the parameters of screen size (*19.3 inches*), resolution (*1280 x 1024*), and refresh rate (*60 Hertz*). The order of stimulus presentation and the stimuli itself (i.e. odor-location pairs within a campus map) were randomized and counterbalanced across participants.

Food odors. A set of four odor solutions was selected to represent each caloric density – taste condition (**Table 2.1**). High- and low-calorie items were defined according to the same energy density cut-offs as in Study 1, using information from The Dutch Food Consumption table and/or USDA Food Composition Databases (RIVM,

2011; USDA Food Composition Databases, 2018). Odor solutions were diluted to medium-high perceived intensity (55-75 mm on a 100mm VAS) and presented to participants in (unlabeled) individual brown bottles (50ml) at a volume of 15ml each. In addition, odor stimuli were piloted in a separate sample of individuals (N=30, 89% female; Age range = 18-35 years) to ensure consistent matching between an odor and its food product, and correct perceptions of caloric density and taste parameters (see pilot questionnaire in the Supplementary Material (**Appendix Chapter 2**)).

Results revealed the final selection of high-calorie odors was rated higher on caloric content ($M = 73.03$ mm, $SD = 17.27$) compared to the low-calorie group ($M = 32.80$ mm, $SD = 24.24$), $t(129) = 16.65$, $p < .001$. Likewise, taste perceptions were congruent with expectations as sweet odors were rated higher on sweetness (Sweet: $M = 79.32$ mm, $SD = 16.93$; Savory: $M = 26.80$ mm, $SD = 25.94$), $Z = -9.77$, $p < .001$, while savory odors scored greater on savoriness ratings (Savory: $M = 66.90$ mm, $SD = 28.25$; Sweet: $M = 14.06$ mm, $SD = 15.96$), $Z = -9.72$, $p < .001$.

Procedure

Prior to testing, participants were informed that the experiment aimed to investigate individuals' memory for specific odors. As in Study 1, this cover story did not explicitly mention the spatial faculty of memory and was successful in diffusing suspicions on the true study aims as revealed in post-hoc (open-ended funneling) debriefing interviews. Participants were likewise informed that good performance would earn them the chance to win an additional reward at the end of the experiment. Hunger states were standardized before test sessions in the same manner as in Study 1. Furthermore, individuals were asked to refrain from using scented products (e.g. perfume) on test days, and consuming scented items (e.g. chewing gum) starting an hour before their test sessions.

The experimental paradigm was identical to that of Study 1, except waist circumference was additionally collected at the onset of testing. Participants were also required to perform an odor recognition memory task following completion of the spatial memory task in each caloric density - taste condition. Furthermore, participants completed the *Macronutrient and Taste Preference Ranking Task* (de Bruijn *et al.*, 2017) prior to answering questions on healthy eating goals in the second test session.

Table 2.1. Food odors used in the present study.

<i>Caloric Density- Taste Condition</i>	<i>Odor Quality</i>	<i>Kcal/100g food counterpart</i>	<i>Company</i>	<i>IPC</i>	<i>Concentration (%) in solvent</i>
<i>H_SW</i>	Chocolate	531 ^a	IFF ^c	10810180	5% in PG ^d
<i>H_SW</i>	Caramel (Dulce de Leche)	382 ^b	IFF	15062070	4% in PG
<i>H_SW</i>	Vanilla	288 ^b	IFF	10860896	4% in PG
<i>H_SW</i>	Apple bake	237 ^b	IFF	10927267	3.4% in PG
<i>H_SA</i>	Butter Popcorn	535 ^b	IFF	10922603	2% in PG
<i>H_SA</i>	Roast Beef	236 ^b	IFF	10924987	0.04% in demi water
<i>H_SA</i>	Roasted Peanuts	577 ^a	IFF	10809896	1% in PG
<i>H_SA</i>	Bacon	505 ^a	IFF	SC753578	0.20% In demi water
<i>L_SW</i>	Melon	30 ^a	IFF	15025874	2% in PG
<i>L_SW</i>	Pineapple	57 ^a	IFF	10866148	1% in PG
<i>L_SW</i>	Pear	55 ^a	IFF	10809904	1% in PG
<i>L_SW</i>	Blackcurrant	53 ^a	IFF	10810572	0.80% in PG
<i>L_SA</i>	Asparagus	19 ^a	IFF	SC753579	0.04% in demi water
<i>L_SA</i>	Cucumber	13 ^a	IFF	15311331	100%
<i>L_SA</i>	Tomato	20 ^a	IFF	10939812	0.03% in PG
<i>L_SA</i>	Mushroom	18 ^a	Givaudan	P-136293	0.04% in demi water

^a From The Dutch Food Consumption Table (RIVM, 2011)^b From the USDA Food Composition Databases (USDA Food Composition Databases, 2018)^c International Flavors and Fragrances^d Propylene Glycol

Measurements

Primary outcome variables. *Spatial memory accuracy* for (sweet/savory) high- and low-calorie foods, as well as *spatial memory bias for high-calorie foods*, was operationalized using Euclidian distances (D) in the same manner as in Study 1 (cf. Allan & Allan, 2013; Nairne *et al.*, 2012). Based on findings of the previous experiment, *spatial memory bias for savory-tasting foods* was additionally calculated as the average

discrepancy in spatial memory accuracy between savory- versus sweet-tasting items ($D_{\text{savory}} - D_{\text{sweet}}$). Accordingly, negative values indicate an enhanced spatial memory for savory-tasting foods.

Secondary outcome variables. Individual *preferences* for respective caloric density and taste food categories were determined using an adapted version of the Macronutrient and Taste Preference Ranking Task [MTPRT], ran on E-prime version 2.0 (de Bruijn *et al.*, 2017). The MTPRT consists of three parts: practicing, liking, and ranking. For the “liking” portion, individuals are introduced to all 32 food images available and required to provide liking ratings on them (100mm VAS anchored from “Do Not Like At All” to “Like Extremely”). The subsequent “ranking” portion of the original task encompasses two sections, one focused on macronutrients and the other on taste. In both sections, individuals are presented with four food images in a number of trials and asked to rank products on each trial in order of “what they most desire to eat at this moment”, beginning with the most desired product. Utilizing the same principles, a subset of 16 products (eight high- and eight low-caloric density) from the original selection of food images was used to construct a (new) caloric density section of the ranking task. In each of eight trials, the four presented food images came from both caloric density categories – with a sweet and savory counterpart for each category. The order in which categories were displayed on the screen was randomized and counterbalanced; both caloric density categories appeared four times in each of the available four image positions. All images were presented twice, on two different positions. Preference scores for respective macronutrient and taste categories were computed using ranking frequencies and formulas from the original authors (see de Bruijn *et al.*, 2017), in which a higher rank corresponded to a higher preference score. Accordingly, the preference for high- (or low-) calorie foods in the newly added caloric density section was tabulated as: $(4 * (\# \text{rank}1) + 3 * (\# \text{rank}2) + 2 * (\# \text{rank}3) + 1 * (\# \text{rank}4) / 16)$.

Waist circumference (mm) was collected with a measuring tape at the midpoint between the lowest rib and the iliac crest, in line with World Health Organization guidelines. Similarly, height (*m*) and weight (*kg*) measures were collected with an electronic scale (SECA 704) and stadiometer (SECA 213) to obtain accurate *BMI (kg/m²)* values.

Predictor variables. Individual predispositions for *Restrained* and *External Eating* were measured as in Study 1 (Cronbach's $\alpha = .84$ and $.75$, respectively) (van Strien *et al.*, 1986). Furthermore to remain consistent with Study 1, we aggregated scores of the three BAS subscales to form a more reliable total BAS measure (Cronbach's $\alpha = .78$) for *Reward Sensitivity* (Carver & White, 1994). In doing so, the number of parameters to be estimated in statistical models was also favorably reduced relative to our sample size.

Control measures. To control for effects of (odor) recognition memory on spatial memory performance, we required individuals to discriminate between four "known" (target) and four "novel" (distractor) food odors in an *odor recognition memory* task following spatial memory tasks (Brünner *et al.*, 2015; Krasnow *et al.*, 2011). A fixed presentation order of target and distractor food odors was (randomly) generated for each caloric density - taste condition. Odor recognition memory scores were calculated as the proportion of odors correctly classified within a condition: correctly recognized target odors (0-4) plus correctly recognized distractor odors (0-4), divided by the total number of targets and distractors (8). To account for extraneous effects of 'liking' or 'wanting' of food types on spatial memory accuracy, we instructed participants to additionally rate how much they liked each odor – as well as their desire to eat the food item associated with an odor – on a 100mm VAS (anchored from "Not At All" to "Very Much"; see Food Stimuli Ratings in the Supplemental Material (**Appendix Chapter 2**)) during the odor recognition memory task (Brünner *et al.*, 2015).

Analogous to Study 1, *Neighborhood SES*, *Subjective SES*, *Healthy Eating Goals*, and *Perceived Performance* were recorded. Finally, a general questionnaire documented both pertinent demographic characteristics (e.g. *Sex*, *Age*) and *Hunger* states (100mm VAS anchored from "Not At All" to "Very Much") at encoding.

Data Analysis

Data were analyzed using IBM SPSS Statistics 23 with statistical significance defined as $p < .05$. With regards to linear mixed effects modelling, the model selection procedure as described for Study 1 was applied. Due to an unforeseen error during testing, estimates for spatial memory biases were unable to be computed for one participant. Consequently, only data from 87 participants were used in the second statistical analysis onwards. As in Study 1, hypotheses and statistical analyses were formulated prior to accessing data.

Caloric density, taste, person-specific factors, and odor-cued food spatial memory accuracy (H_{1A} and H₂). To determine whether the accuracy of odor-cued food spatial memory varies with caloric content or taste aspects, we formulated a random intercept and slope linear mixed model with main and interaction effects of *Caloric Density* and *Taste* as fixed factors, *Participant* and *Test Session* as random factors (covariance structure: Unstructured), *Sex*, *Age*, *Neighborhood SES*, *Subjective SES*, *Taste Order*, *Liking*, *Desirability*, *Odor recognition memory scores* and *Hunger scores* as covariates, and *Spatial Memory Accuracy (D)* as the dependent variable.

To examine person-specific factors that could predict the magnitude of (odor-cued) food spatial memory accuracy, we included main and interaction effects (with *Caloric Density*) of *Restrained Eating*, *External Eating*, and *Reward Sensitivity* as predictor variables.

Spatial memory biases and food preferences (H_{1B}). To determine whether the high-calorie bias in (odor-cued) spatial memory predicted an increased preference for high-calorie foods, we formulated a multiple linear regression model (N=1; simultaneous entry method) with *Sex*, *Age*, *Neighborhood SES*, *Subjective SES*, *Restrained Eating*, *External Eating*, *Reward Sensitivity*, *Liking of High- versus Low-calorie food odors*, *Desirability of High- versus Low-calorie food odors*, *Hunger ratings of the final test session*, *Healthy Eating Goals*, and *Spatial Memory Bias for High- versus Low-calorie food odors* ($D_{\text{High Calorie}} - D_{\text{Low Calorie}}$) as predictor variables, and the relative preference of *High- versus Low-calorie foods* ($\text{Preference}_{\text{High Calorie}} - \text{Preference}_{\text{Low Calorie}}$) as the dependent variable.

To determine whether the savory-taste bias in (odor-cued) spatial memory predicted an increased preference for savory-tasting foods, we formulated a multiple linear regression model (N=1; simultaneous entry method) with *Sex*, *Age*, *Neighborhood SES*, *Subjective SES*, *Liking of Savory- versus Sweet-tasting food odors*, *Desirability of Savory- versus Sweet-tasting food odors*, *Healthy Eating Goals*, and *Spatial Memory Bias for Savory- versus Sweet-tasting food odors* ($D_{\text{Savory}} - D_{\text{Sweet}}$) as predictor variables, and the relative preference of *Savory- versus Sweet-tasting foods* ($\text{Preference}_{\text{Savory}} - \text{Preference}_{\text{Sweet}}$) as the dependent variable.

Spatial memory bias for high-calorie foods and long-term dietary intake (H_{1B}). Multiple linear regressions (N=2; simultaneous entry method) were

performed on *BMI* and *Waist Circumference*, with *Sex*, *Age*, *Neighborhood SES*, *Subjective SES*, *Restrained Eating*, *External Eating*, *Reward Sensitivity*, *Liking of High- and Low-calorie food odors*, *Desirability of High- and Low-calorie food odors*, *Healthy Eating Goals*, and *Spatial Memory Accuracy (High- and Low-calorie food odors)* as predictor variables.

Similarly, final multiple linear regression models ($N=2$; simultaneous entry method) were formulated to take into account the relative effects of high- and low-calorie (odor-cued) food spatial memory on *BMI* and *Waist Circumference*. Accordingly, *Sex*, *Age*, *Neighborhood SES*, *Subjective SES*, *Restrained Eating*, *External Eating*, *Reward Sensitivity*, *Liking of High- versus Low-calorie food odors*, *Desirability of High- versus Low-calorie food odors*, *Healthy Eating Goals*, and *Spatial Memory Bias for High- versus Low-calorie food odors* ($D_{\text{High Calorie}} - D_{\text{Low Calorie}}$) were entered as independent variables.

Results

Odor-cued Food Spatial Memory: Accuracy and Biases

The average pointing error in odor-cued food spatial memory across all caloric density-taste conditions was 135.49 pixels (95% CI = [126.74, 144.25]). Correcting for differences in resolution, exploratory analysis revealed this represented a significant, but minor, increase from that observed in Study 1 with visual food cues, $F(1, 184) = 7.87$, $p = .006$, $\eta^2 = 0.04$, 90% CI η^2 [0.007, 0.10]. Perceived performance ratings had a medium negative correlation with actual pointing errors ($r_s(346) = -.31$; $p < .001$). *Perceived performance did not differ between caloric density conditions (Mean difference_{High-Low calorie} = 3.28 mm, 95% CI = [-2.11, 8.68]), $t(86) = 1.21$, $p = .230$, $d = 0.13$, but did vary significantly between taste conditions (Mean difference_{Sweet-Savory} = -6.39 mm, 95% CI = [-10.98, -1.81]), $t(86) = -2.77$, $p = .007$, $d = 0.30$.*

Overall, individuals displayed a greater accuracy in odor-cued food spatial memory for high-calorie food odors (i.e. smaller pointing error or D) relative to low-calorie odor counterparts, $F(1, 1240) = 18.43$, $p < .001$, $\eta^2 = 0.01$, 90% CI η^2 [0.006, 0.03] (**Figure 2.3**).

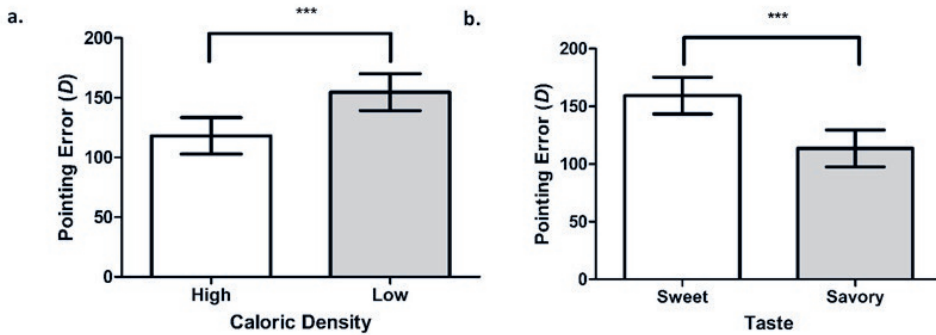


Figure 2.3. Odor-cued spatial memory for (a) Caloric Density and (b) Taste food groups. Spatial memory accuracy was operationalized as the “pointing error” or distance in pixels (D) between true and indicated food locations, with lower D values denoting a higher accuracy in (odor-cued) food spatial memory. A triple asterisk indicates a significant difference with a p value lower than .001. Error bars represent 95% confidence intervals.

Similarly, savory food odor locations were more accurately recalled than sweet alternatives, $F(1,1309) = 23.00$, $p < .001$, $\eta^2 = 0.02$, 90% CI η^2 [0.007, 0.03]. These effects persisted regardless of demographics (e.g. Sex), hedonic evaluations of odors, or odor recognition memory scores. Furthermore, exploratory analysis revealed that the amount of time participants spent on spatial recall tests significantly (negatively) predicted spatial memory performance ($B = 0.002$, 95% CI = [0.001, 0.003]), $F(1,789) = 7.64$, $p = .006$, $\eta^2 = 0.01$, 90% CI η^2 [0.002, 0.02], but did not account for the observed bias effects.

Taste and Person-specific Moderators

The interaction of Caloric Density and Taste on (odor-cued) spatial memory performance was not significant, $F(1,90.26) = 0.32$, $p = .573$, $\eta^2 = 0.004$, 90% CI η^2 [0, 0.05]. Restrained Eating, External Eating, Reward Sensitivity and corresponding interactions (with Caloric Density) were similarly not associated with (odor-cued) food spatial memory accuracy (all $p > .05$; $\eta^2 = 1 \times 10^{-4}$ [0, 0.003], 0.003 [0, 0.01], and 1×10^{-4} [0, 0.003], respectively).

Spatial Memory Biases and Food Preferences

From the tested set of predictors, the high-calorie bias in (odor-cued) food spatial memory was not significantly associated with an increased preference for high-calorie foods ($B = -0.001$, 95% CI = [-0.003, 0.001]), $t(74) = -1.44$, $p = .08$. On the other hand, an individual’s Healthy Eating Goals correlated negatively with high-calorie food preferences ($B = -0.29$, 95% CI = [-0.54, -0.04]), $t(74) = -2.32$, $p = .023$.

With respect to preference biases towards savory-tasting foods, none of the entered predictors captured meaningful variation in measured responses (all $p > .05$) – including the savory-taste bias in (odor-cued) food spatial memory ($B = -0.001$, 95% CI = $[-0.002, 0.001]$), $t(78) = -0.66$, $p = .257$.

Spatial Memory Bias for High-calorie Foods in relation to BMI and Waist Circumference

Spatial memory for high-calorie food odors was not associated with BMI ($B = 0.002$, 95% CI = $[-0.01, 0.01]$), $t(72) = 0.53$, $p = .601$, or waist circumference ($B = 0.02$, 95% CI = $[-0.14, 0.18]$), $t(72) = 0.25$, $p = .801$. Likewise, spatial memory for low-calorie food odors was not predictive of BMI ($B = 0.001$, 95% CI = $[-0.01, 0.01]$), $t(72) = 0.29$, $p = .775$, or waist circumference ($B = 0.03$, 95% CI = $[-0.10, 0.17]$), $t(72) = 0.49$, $p = .623$. The high-calorie bias in (odor-cued) spatial memory also did not systematically covary with BMI ($B = 0.001$, 95% CI = $[-0.004, 0.01]$), $t(75) = 0.29$, $p = .388$, or waist circumference ($B = 0.001$, 95% CI = $[-0.12, 0.12]$), $t(75) = 0.01$, $p = .496$. On the contrary, an individual's Healthy Eating Goals, Restrained Eating tendencies, and Liking (bias) for high-calorie food odors proved to be robust correlates of both measures across all statistical models (see **Tables A2.2** and **A2.3** in the Supplemental Material).

General Discussion

Across two lab studies that engaged distinct sensory modalities, while controlling for consciously mediated valuations or personal experiences with foods, individuals more accurately recalled the locations of high-calorie and savory-tasting foods (H_{1A}). These findings support an adaptive account of human memory and are compatible with the notion that spatial processing tendencies optimized for fluctuating ancestral food habitats may be preserved. However, the more accurate localization of high-calorie foods did not differ for sweet or savory foods, or across an individual's trait eating style or degree of reward sensitivity (H_2). Furthermore, effects of biases in food spatial memory were not present on eating-related parameters of food preference, food choice, BMI, and waist circumference (H_{1B}).

In line with New *et al.* (2007b), we found that individuals showcased a more accurate memory for the locations of high-calorie foods, irrespective of factors that may have accounted for a general learning mechanism (e.g. encoding time, personal affinities with foods). It is equally unlikely that this difference arose from a higher

attractiveness or visual salience of high-calorie food stimuli, as parallel results were obtained with olfactory food cues at similar perceived intensities. Notably, vision and olfaction are distant senses important for detecting food sources in the environment and directing eating behavior towards signaled products (McCrickerd & Forde, 2016; Ramaekers *et al.*, 2014). Complementing these roles, our findings corroborate the efficacy of both sensory modalities in signaling important nutritional characteristics of food sources and serving as associative cues in support of spatial navigation (Dahmani *et al.*, 2018; McCrickerd & Forde, 2016; Schifferstein *et al.*, 2009). The slight advantage of vision over olfaction observed in spatial memory performance may be attributed to a greater tendency and fluency of sighted-individuals to internally represent spatial information in visual terms, or an overall greater difficulty of assigning verbal labels to (and identifying) odors (Cain, 1979; Schifferstein *et al.*, 2009). Interestingly, further reinforcing the results of New *et al.* (2007b), the high-calorie bias in spatial memory was not influenced by sex. Although sex differences in spatial abilities are widely documented in literature (Silverman & Eals, 1992; Silverman *et al.*, 2007), this finding makes sense from an evolutionary perspective, as the adaptive ancestral problem of efficiently (re)locating and exploiting high quality nutritional resources would have impinged similarly on both sexes – resulting in a sexually monomorphic but domain-specific spatial processing mechanism (Cosmides & Tooby, 2013; Krasnow *et al.*, 2011).

A novel main effect of taste on spatial memory accuracy was additionally elucidated as individuals better remembered locations of savory- (versus sweet-) tasting foods – regardless of caloric content. Within the framework of adaptive memory (Nairne & Pandeirada, 2008b; Nairne & Pandeirada, 2010), our results suggest that the attainment of sufficient protein (relative to carbohydrates) may have posed a bigger adaptive problem faced by our hunter-gatherer ancestors. In support of this notion, ancestral protein consumption is estimated to have encompassed a substantial 30% of a 3000 kcal/day diet (Cordain *et al.*, 2000; Eaton, 2006). This high demand coupled with a high variance in return rates of major protein sources (i.e. mobile animal prey), would have garnered a greater difficulty with meeting protein intake requirements relative to carbohydrates – the latter mainly sourced from (immobile) fruits and vegetables (Bird *et al.*, 2009; Eaton, 2006). Therefore, we speculate that a bias in location memory for savory-tasting foods may be the expression of a fitness advantage that facilitated a more lucrative pursuit of protein-rich resources. Relatedly, studies have shown that

human visual attention and episodic memory are especially adept at processing information on self-propelling animate (e.g. animals) versus inanimate objects, potentially reflecting a survival mechanism to readily detect prey or predators in the environment (Nairne *et al.*, 2017; New *et al.*, 2007a). Moreover, protein intake has been demonstrated to be tightly regulated in humans across time and geographical conditions, and even “leveraged” or prioritized over the consumption of other macronutrients when nutritional intake targets are not met (Cordain *et al.*, 2000; Simpson & Raubenheimer, 2005). A compensatory pathway for restoring protein balance involves the activation of (implicit) cognitive processes that orient food preferences and choice behavior towards savory high-protein foods (Griffioen-Roose *et al.*, 2012; Griffioen-Roose *et al.*, 2014). Taken together, these observations add empirical weight to the idea that a savory-taste bias in human spatial memory may have been functionally selected for maintaining adequate protein status.

In light of the difficulties associated with establishing a definitive evolutionary account of our findings, our data enable us to rule out a couple alternative explanations for the observed biases in human food spatial memory. The possibility that the high-calorie bias arose from a conscious effort of (health-minded) individuals to strategically avoid high-calorie food locations can be countered with exploratory analyses that revealed healthy eating goals were not a significant predictor of food spatial memory accuracy in both studies. Indeed, such an “adaptive avoidance” hypothesis, in which (dieting) individuals with the high-calorie bias would adaptively avoid high-calorie food locations and have a lower BMI, is not supported by the existing literature (Allan & Allan, 2013). It is also conceivable to suspect that within-experimental differences in nameability or depth of processing accounted for discrepancies in spatial memory performance – congruent with the (domain-general) levels of processing framework. By this account, high-calorie and savory-tasting food locations were better recalled because they were inherently easier to assign meaning to (Craik & Lockhart, 1972). However, this prospect is unlikely as we controlled for individual experience with a food through familiarity ratings (Study 1) and odor recognition memory scores (Study 2), the latter of which is known to positively covary with odor knowledge and odor naming abilities (Frank *et al.*, 2010).

Although biases in human food spatial memory are clearly expressed, their translation into actual eating behavior was not detected in the present work. In light of

observed effect sizes, potential relationships with long-term dietary intake are also likely to be small in magnitude. This gap may be attributed to a variety of reasons. As the measurement of anthropometrics temporally preceded the selection of foods, individuals may have been primed with a dieting or health goal, thus potentially diluting effects on subsequent (high-calorie) food preference and choice (van der Laan *et al.*, 2017). However, the one-week washout period and other implemented controls (e.g. anonymity/honesty reminders; covert nature of the food choice task) would have helped in mitigating any substantial confounding effects. In addition, as the current techniques used to assess food choice lacked external validity, and food spatial memory biases are thought to exert their influence by affording a greater navigational convenience, (pronounced) effects may only be present in more naturalistic food settings that allow for navigation within a bigger scale of space. Theoretical considerations are also merited, as contrary to Allan & Allan (2013), an individual's reported healthy eating intentions – rather than the high-calorie spatial memory bias – was a robust predictor of both short- and long-term parameters of eating behavior. This suggests that obesogenic effects of the high-calorie bias may be effectively countered by an individual's explicit health attitudes and self-regulation capacity – in a manner resonant with dual-processing theories of cognition (Evans, 2003). The potential link between the high-calorie spatial memory bias and obesogenic behaviors may therefore be a more nuanced process that recruits higher-order cognitive constructs.

Finally, it would be worthwhile to explore the cognitive processes underlying food spatial memory biases. The majority of our results concerning encoding times and perceived performance ratings propose a link with more implicit mechanisms. It would therefore be interesting to see whether food-related attention biases, specifically in the orientation phase of attention, covary with the expression of these cognitive biases. These results could yield important insights to supplement existing interventional strategies aimed at decreasing cognitive reactivities to high-calorie food stimuli, in an effort to promote dietary regulation.

In closing, our work highlights that content matters deeply for the faculty of human food spatial memory. Findings are reminiscent of a cognitive system presumably attuned to ancestral priorities of optimal foraging: one capable of assessing the profitability of encountered food resources and preferentially processing the locations

of those higher in nutritional quality – in an implicit manner that does not compete for volitional attention. Knowledge of these biases in human food spatial memory and their associated (proximal) mechanisms could inform new strategies to promote healthier eating behavior within the evolutionary novel “obesogenic” food landscape.

Acknowledgements

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Chapter 2

Appendix

Food Pics Catalogue Numbers

H_SW: 16, 41, 44, 103, 116, 134, 189, 286, 313, 344, 400, 507; *H_SA*: 2, 27, 53, 60, 104, 186, 350, 416, 489, 517, 519, 555; *L_SW*: 199, 241, 255, 285, 386, 389, 392, 393, 407, 413, 453, 466; *L_SA*: 233, 250, 251, 258, 260, 264, 265, 274, 333, 335, 364, 442

Study 1 Pilot Questionnaire

Instructions: Answer all of the required questions. There are no correct or incorrect responses, we are interested in hearing your opinions. Do not overthink your answers; your first impression is usually the best.

1. How many **CALORIES** do you think the product consists of?

Very few calories | _____ | Many calories

2. How **SWEET** do you think the product tastes?

Not at all | _____ | Very sweet

3. How **SAVORY** do you think the product tastes?

Not at all | _____ | Very savory

4. How **HEALTHY** do you think the product is?

Not at all | _____ | Very healthy

Study 2 Pilot Questionnaire

Instructions: For each of the following odors, answer all of the required questions by placing a vertical bar (|) on the lines below. Please take some time between odors. There are no correct or incorrect responses, we are interested in hearing your opinions. Do not overthink your answers; your first impression is usually the best.

1. How **INTENSE** do you find the odor?

Not at all | _____ | Very much

2. How many **CALORIES** do you think a product (with this odor) consists of?

Very few calories |-----| *Many calories*

3. How **SWEET** do you think a product (with this odor) tastes?

Not at all |-----| *Very sweet*

4. How **SAVORY** do you think a product (with this odor) tastes?

Not at all |-----| *Very savory*

5. Which one of the following products best **MATCH** the odor (circle one)?

Apple pie/bake	Blackcurrant	Cucumber	Pineapple
Asparagus	Butter popcorn	Melon	Roast Peanuts
Bacon	Caramel	Mushroom	Tomato
Beef	Chocolate	Pear	Vanilla

Food Stimuli Ratings

Study 1

Instructions: Please answer the questions below for all foods. Your first impression is usually the best; there are no right or wrong answers.

1. How much do you desire to eat the displayed food at this moment?

Not at all |-----| *Very much*

2. How familiar are you with the displayed food item?

1 2 3 4 5

1= I do not recognize the product; 2= I recognize the product, but I have not tasted it; 3= I have tasted; 4= I occasionally eat the product; 5= I regularly eat the product

Study 2

Instructions: For each of the following odors, please indicate whether you previously smelled them in the task before (= “old”) or not (= “new”) by **circling your answer**. Also rate how much you **like** the odor and your **desire to eat the food item** associated with the odor. Please take a small break, and smell the inside of your wrist, between odors.

1. This odor is:

Old

New

2. How much do you **like** the odor?

Not at all |—————| Very much

3. How much do you **desire to eat** the food item with this odor at this moment?

Not at all |—————| Very much

Table A2.1.Predicting BMI (kg/m²) from (the high-calorie bias in) food spatial memory, in multiple linear regression models.

Variable	B	95% CI	Beta	<i>t</i>	<i>p</i>	R	R ²
Model 1: BMI and food spatial memory							
Constant	32.15	23.77 – 40.53		7.64	.000***	.59	.35
Sex ^a	-1.46	-2.55 – -0.38	-0.31	-2.69	.009**		
Age	-0.02	-0.19 – 0.16	-0.02	-0.17	.868		
Ethnicity	0.13	-0.30 – 0.56	0.07	0.62	.538		
Neighborhood SES	0.11	-0.17 – 0.39	0.08	0.78	.440		
Subjective SES	-0.01	-0.40 – 0.39	-0.003	-0.02	.981		
Restrained Eating	0.60	-0.12 – 1.32	0.18	1.65	.103		
External Eating	-0.29	-1.11 – 0.53	-0.08	-0.71	.483		
Reward Sensitivity	-1.07	-2.45 – 0.30	-0.18	-1.55	.125		
Desirability _{High Calorie}	-0.07	-0.11 – -0.03	-0.53	-3.12	.003**		
Desirability _{Low Calorie}	0.04	-0.004 – 0.08	0.30	1.81	.075		
Familiarity _{High Calorie}	-0.41	-2.27 – 1.45	-0.06	-0.44	.662		
Familiarity _{Low Calorie}	0.42	-1.39 – 2.23	0.07	0.46	.648		
Healthy Eating Goals	-0.70	-1.22 – -0.18	-0.29	-2.66	.010*		
Spatial Memory _{High Calorie} ^b	-0.004	-0.01 – 0.002	-0.17	-1.31	.194		
Spatial Memory _{Low Calorie} ^b	0.002	-0.004 – 0.01	0.08	0.64	.527		
Model 2: BMI and the high-calorie bias in spatial memory							
Constant	30.85	23.45 – 38.24		8.31	.000***	.56	.31
Sex ^a	-1.29	-2.32 – -0.25	-0.27	-2.47	.016*		
Age	-0.01	-0.19 – 0.17	-0.01	-0.10	.923		
Ethnicity	0.07	-0.35 – 0.49	0.04	0.32	.748		
Neighborhood SES	0.10	-0.18 – 0.37	0.07	0.69	.490		
Subjective SES	-0.06	-0.44 – 0.32	-0.03	-0.33	.743		
Restrained Eating	0.52	-0.19 – 1.24	0.16	1.45	.151		
External Eating	-0.42	-1.22 – 0.38	-0.11	-1.04	.302		
Reward Sensitivity	-0.94	-2.31 – 0.43	-0.16	-1.37	.176		
Desirability _{High – Low Calorie}	-0.05	-0.09 – -0.01	-0.35	-2.60	.011*		
Familiarity _{High – Low Calorie}	-0.34	-2.00 – 1.33	-0.05	-0.40	.690		
Healthy Eating Goals	-0.67	-1.19 – -0.15	-0.28	-2.57	.012*		
High-calorie Spatial Memory Bias ^c	-0.003	-0.01 – 0.002	-0.12	-1.18	.244		

^a Males are the reference group^b *D* or pointing error (Lower values denote a greater accuracy in spatial memory)^c $D_{\text{High Calorie}} - D_{\text{Low Calorie}}$ (Lower values denote a greater bias in spatial memory for high-calorie foods)* $p < .05$; ** $p < .01$; *** $p < .001$

Table A2.2.

Predicting BMI (kg/m²) from (the high-calorie bias in) odor-cued food spatial memory, in multiple linear regression models.

Variable	B	95% CI	Beta	<i>t</i>	<i>p</i>	R	R ²
Model 1: BMI and (odor-cued) food spatial memory							
Constant	16.14	8.19 – 24.09		4.05	.000***	.66	.44
Sex ^a	-0.89	-2.09 – 0.31	-0.16	-1.47	.145		
Age	0.17	-0.07 – 0.41	0.15	1.45	.152		
Neighborhood SES	0.01	-0.30 – 0.32	0.01	0.06	.950		
Subjective SES	0.01	-0.43 – 0.44	0.003	0.03	.973		
Restrained Eating	1.96	1.23 – 2.70	0.52	5.31	.000***		
External Eating	-0.52	-1.57 – 0.53	-0.11	-0.98	.328		
Reward Sensitivity	0.76	-0.37 – 1.88	0.12	1.34	.183		
Liking _{High Calorie}	0.14	0.06 – 0.23	0.81	3.29	.002**		
Liking _{Low Calorie}	-0.04	-0.12 – 0.05	-0.18	-0.83	.411		
Desirability _{High Calorie}	-0.12	-0.19 – -0.04	-0.82	-3.05	.003**		
Desirability _{Low Calorie}	0.05	-0.03 – 0.13	0.32	1.34	.184		
Healthy Eating Goals	-0.72	-1.28 – -0.16	-0.26	-2.54	.013*		
Spatial Memory _{High Calorie} ^b	0.002	-0.01 – 0.01	0.05	0.53	.601		
Spatial Memory _{Low Calorie} ^b	0.001	-0.01 – 0.01	0.03	0.29	.775		
Model 2: BMI and the high-calorie bias in (odor-cued) food spatial memory							
Constant	17.15	9.02 – 25.28		4.20	.000***	.61	.37
Sex ^a	-0.84	-2.07 – 0.39	-0.15	-1.36	.178		
Age	0.25	0.02 – 0.48	0.21	2.13	.036*		
Neighborhood SES	-0.04	-0.36 – 0.27	-0.03	-0.26	.797		
Subjective SES	0.002	-0.44 – 0.44	0.001	0.01	.993		
Restrained Eating	1.97	1.21 – 2.73	0.53	5.17	.000***		
External Eating	-0.21	-1.20 – 0.78	-0.04	-0.42	.678		
Reward Sensitivity	0.54	-0.61 – 1.69	0.09	0.93	.353		
Liking _{High – Low Calorie}	0.09	0.01 – 0.17	0.55	2.23	.028*		
Desirability _{High – Low Calorie}	-0.08	-0.15 – -0.01	-0.54	-2.21	.030*		
Healthy Eating Goals	-0.81	-1.38 – -0.23	-0.29	-2.78	.007**		
High-calorie Spatial Memory Bias ^c	0.001	-0.004 – 0.01	0.03	0.29	.776		

^aMales are the reference group

^b*D* or pointing error (Lower values denote a greater accuracy in spatial memory)

^c*D*_{High Calorie} – *D*_{Low Calorie} (Lower values denote a greater bias in spatial memory for high-calorie food odors)

p* < .05; ** *p* < .01; * *p* < .001

Table A2.3.

Predicting waist circumference (mm) from (the high-calorie bias in) odor-cued food spatial memory, in multiple linear regression models.

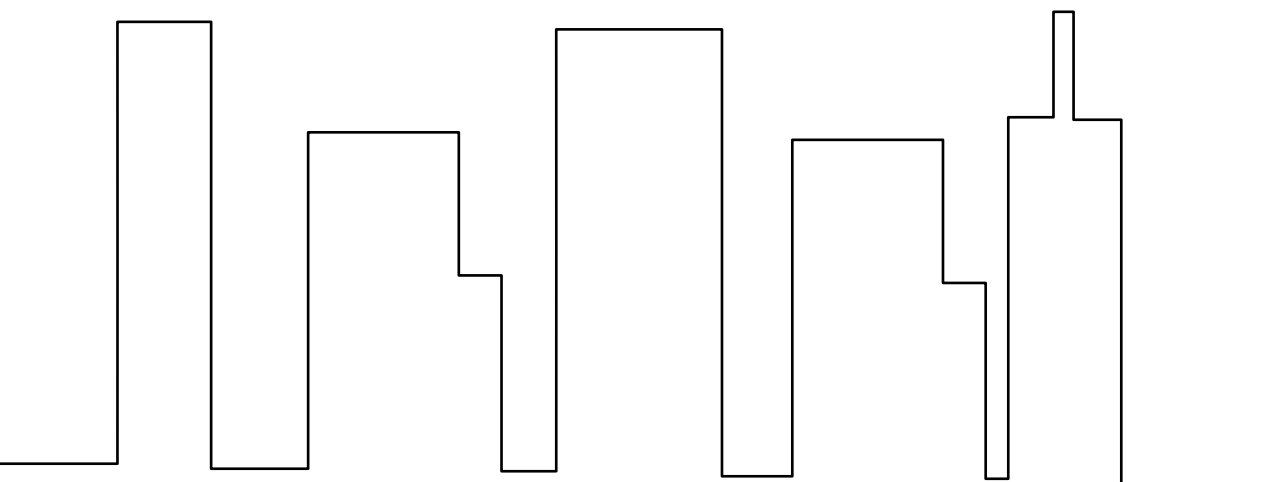
Variable	B	95% CI	Beta	<i>t</i>	<i>p</i>	R	R ²
Model 1: Waist circumference and (odor-cued) food spatial memory							
Constant	644.86	445.23 – 844.49		6.44	.000***	.80	.64
Sex ^a	-90.08	-120.27 – -59.90	-0.51	-5.95	.000***		
Age	8.95	2.99 – 14.91	0.24	2.99	.004**		
Neighborhood SES	-8.82	-16.68 – -0.95	-0.17	-2.23	.029*		
Subjective SES	-2.37	-13.23 – 8.48	-0.03	-0.44	.664		
Restrained Eating	57.17	38.69 – 75.66	0.49	6.17	.000***		
External Eating	9.25	-17.19 – 35.68	0.06	0.70	.488		
Reward Sensitivity	11.51	-16.62 – 39.63	0.06	0.82	.417		
Liking _{High Calorie}	3.40	1.21 – 5.58	0.61	3.10	.003**		
Liking _{Low Calorie}	-1.19	-3.38 – 1.00	-0.19	-1.09	.281		
Desirability _{High Calorie}	-2.59	-4.50 – -0.68	-0.58	-2.70	.009**		
Desirability _{Low Calorie}	0.99	-0.89 – 2.87	0.20	1.05	.299		
Healthy Eating Goals	-29.56	-43.69 – -15.43	-0.34	-4.17	.000***		
Spatial Memory _{High Calorie} ^b	0.02	-0.14 – 0.18	0.02	0.25	.801		
Spatial Memory _{Low Calorie} ^b	0.03	-0.10 – 0.17	0.04	0.49	.623		
Model 2: Waist circumference and the high-calorie bias in (odor-cued) food spatial memory							
Constant	671.73	470.51 – 872.95		6.65	.000***	.78	.60
Sex ^a	-90.12	-120.69 – -59.55	-0.51	-5.87	.000***		
Age	10.21	4.43 – 15.98	0.28	3.52	.001**		
Neighborhood SES	-9.40	-17.18 – -1.61	-0.19	-2.41	.019*		
Subjective SES	-2.47	-13.42 – 8.48	-0.04	-0.45	.655		
Restrained Eating	57.27	38.46 – 76.08	0.49	6.07	.000***		
External Eating	13.39	-11.09 – 37.87	0.09	1.09	.279		
Reward Sensitivity	7.28	-21.22 – 35.78	0.04	0.51	.612		
Liking _{High – Low Calorie}	2.30	0.29 – 4.32	0.45	2.28	.026*		
Desirability _{High – Low Calorie}	-1.74	-3.55 – 0.07	-0.37	-1.92	.059		
Healthy Eating Goals	-31.49	-45.80 – -17.18	-0.36	-4.39	.000***		
High-calorie Spatial Memory Bias ^c	0.001	-0.12 – 0.12	0.001	0.01	.991		

^aMales are the reference group

^b*D* or pointing error (Lower values denote a greater accuracy in spatial memory)

^c*D*_{High Calorie} – *D*_{Low Calorie} (Lower values denote a greater bias in spatial memory for high-calorie food odors)

p* < .05; *p* < .01; ****p* < .001



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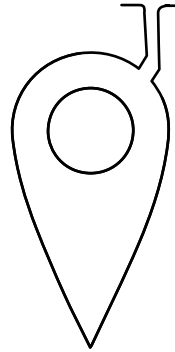
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A minimalist line-art illustration of a city skyline with several rectangular buildings of varying heights. The lines are thin and black, set against a white background.

Chapter 3

Human spatial memory
implicitly prioritizes
high-calorie foods



Abstract

All species face the important adaptive problem of efficiently locating high-quality nutritional resources. We explored whether human spatial cognition is enhanced for high-calorie foods, in a large multisensory experiment that covertly tested the location memory of people who navigated a maze-like food setting. We found that individuals incidentally learned and more accurately recalled locations of high-calorie foods – regardless of explicit hedonic valuations or personal familiarity with foods. In addition, the high-calorie bias in human spatial memory already became evident within a limited sensory environment, where solely odor information was available. These results suggest that human minds continue to house a cognitive system optimized for energy-efficient foraging within erratic food habitats of the past, and highlight the often underestimated capabilities of the human olfactory sense.

Introduction

A recurring fitness-relevant task faced by all species is the efficient pursuit of nutritional resources (Schoener, 1971). A central theorem of optimal foraging theory is that an individual's fitness is a direct function of the efficiency with which one acquires energy, and natural selection pressures favour foraging traits that maximize the net rate of energy gain (Schoener, 1971; Pyke *et al.*, 1977). Although this theory has been extensively referenced in relation to the foraging strategies of other animals (Pyke *et al.*, 1977), the question of whether humans also inherently carry adaptations geared toward energy-efficient foraging has not been thoroughly assessed to date.

For about 99 percent of human evolution, our ancestors were hunter-gatherers inhabiting a highly complex and variable physical food environment, where food sources varied on both spatial and temporal availabilities (New *et al.*, 2007b; Winterhalder, 1981). A cognitive adaptation that could have evolved to optimize foraging efforts within such erratic food habitats of the past is a high-calorie bias in spatial memory (New *et al.*, 2007b; de Vries *et al.*, 2020b). Such an inbuilt spatial bias entails the automatic registration and prioritization in memory of high-calorie food locations. This would have enabled foragers to efficiently navigate toward valuable calorie-dense resources – without competing for limited attentional capacities required in other important activities such as avoiding predation (Krasnow *et al.*, 2011; New *et al.*, 2007b). Indeed, a similar mechanism has been observed in other animal species (Cunningham & Janson, 2007; Janmaat *et al.*, 2014; Janson, 1998). Using an innovative and ecologically valid experimental set-up that covertly tested the food location memory of more than 500 individuals, we provide first-hand evidence that human spatial processing is implicitly biased toward high-calorie foods.

To mirror real-world navigation within a heterogeneous food environment as closely as possible, we created a maze-like setting where participants followed a specific route within a room to sample an assortment of (sweet and savory) high- and low-calorie food stimuli at dispersed pillar locations (**Figure 3.1**). We emulated two sensory environments in separate rooms, each of which engaged sensory modalities fundamental to the processes of spatial navigation and eating behavior (Boesveldt & de Graaf, 2017; Jacobs, 2012; Yarmolinsky *et al.*, 2009): In the *multisensory environment* (i.e. vision + taste + olfaction), stimuli consisted of actual food products that individuals had to eat, whereas individuals were instructed to only smell food odors in the *olfactory*

environment. Importantly, participants were not informed that their (spatial) memory would be tested afterwards, to ensure that the encoding of food locations would be purely incidental. We then compared performance, expressed as the proportion of correct food-to-pillar relocations in a surprise spatial memory task, for high-calorie versus low-calorie food stimuli in both sensory environments.

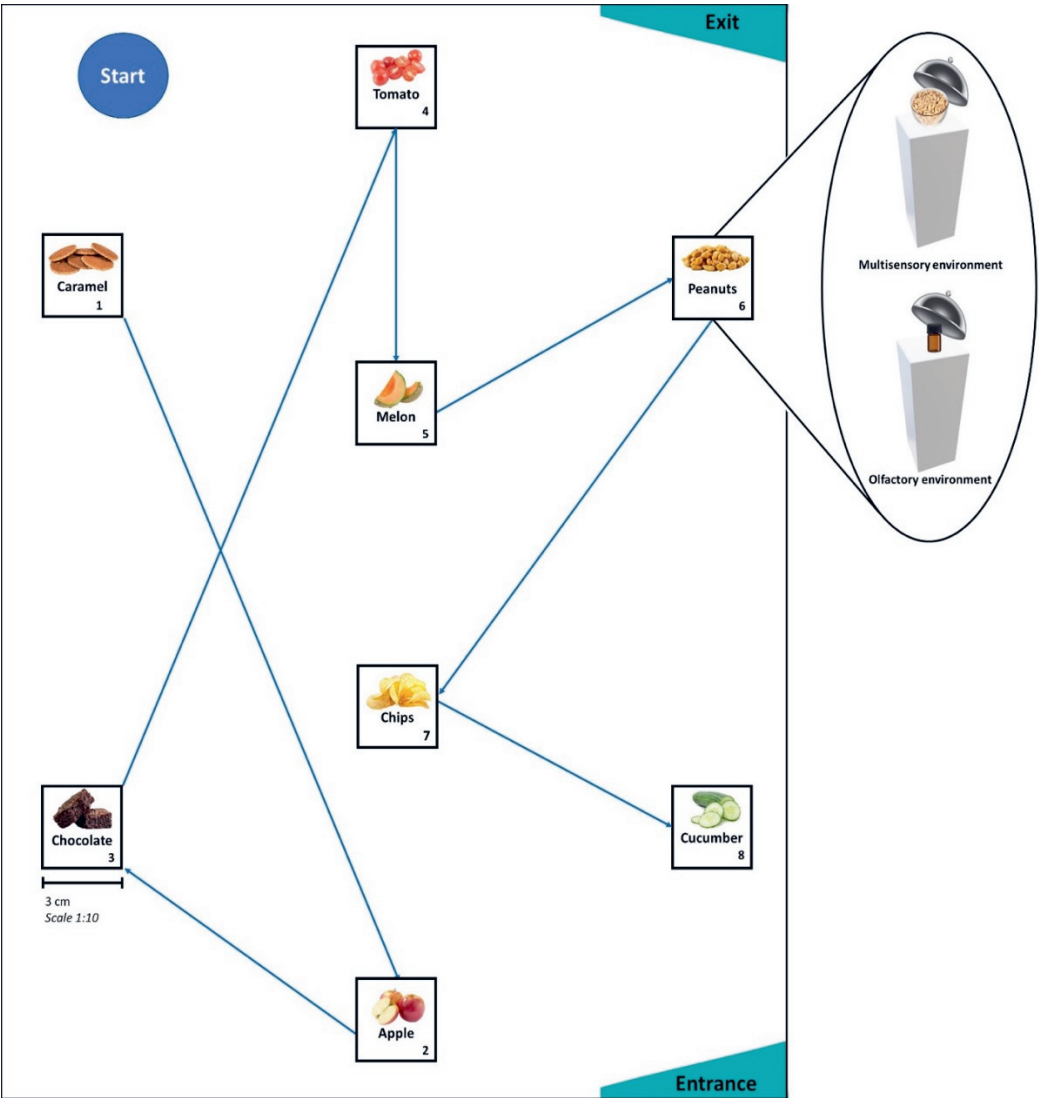


Figure 3.1. Heterogeneous food environment. Example of the spatial distribution of food stimuli and navigation route within the maze-like experimental setting.

Results

Human Spatial Memory Automatically Prioritizes High-calorie Food.

In the multisensory environment, individuals relocated high-calorie foods to correct pillar locations significantly more frequently than low-calorie alternatives (High-calorie: $M = 0.63$, 95% CI = [0.58,0.67]; Low-calorie: $M = 0.57$, 95% CI = [0.52,0.62]), $\chi^2(1) = 9.35$, $p = .002$, OR = 1.27, 95% CI = [1.09, 1.48] (**Figure 3.2**). This effect occurred regardless of demographics, relevant state characteristics (e.g. hunger and alertness), hedonic evaluations of foods (i.e. liking and desirability ratings; **Figure 3.3**), and familiarity with foods. Similarly, individuals in the olfactory environment more frequently relocated odors signaling high-calorie foods to correct pillar locations relative to low-calorie odor counterparts (High-calorie: $M = 0.36$, 95% CI = [0.33,0.39]; Low-calorie: $M = 0.30$, 95% CI = [0.27,0.34]), $\chi^2(1) = 6.88$, $p = .009$, OR = 1.28, 95% CI = [1.06, 1.54] (**Figure 3.2**), while controlling for the same set of potential confounders – although the likelihood of a correct relocation increased with a greater familiarity with an odor stimulus, $\chi^2(1) = 47.31$, $p < .001$, OR = 3.55, 95% CI = [2.47,5.09]. Conversely, spatial memory accuracy did not vary according to the taste of a food (i.e. sweet or savory) in either sensory condition.

The High-calorie Bias in Human Spatial Memory Manifests with Limited Sensory Information.

In a combined analysis of both sensory conditions, a better *overall* food relocation performance was observed in the multisensory compared to the olfactory environment (Multisensory: $M = 0.58$, 95% CI = [0.54,0.61]; Olfactory: $M = 0.36$, 95% CI = [0.33,0.39]), $\chi^2(1) = 62.95$, $p < .001$, OR = 2.43, 95% CI = [1.95,3.03], after adjusting for differences between participant samples (**Figure 3.2**). However, the sensory nature of food stimuli did not moderate the effect of caloric density on spatial memory accuracy, $\chi^2(1) = 0.49$, $p = .486$, indicating that the high-calorie spatial memory bias was equally expressed in both sensory environments – even where solely odor information was available.

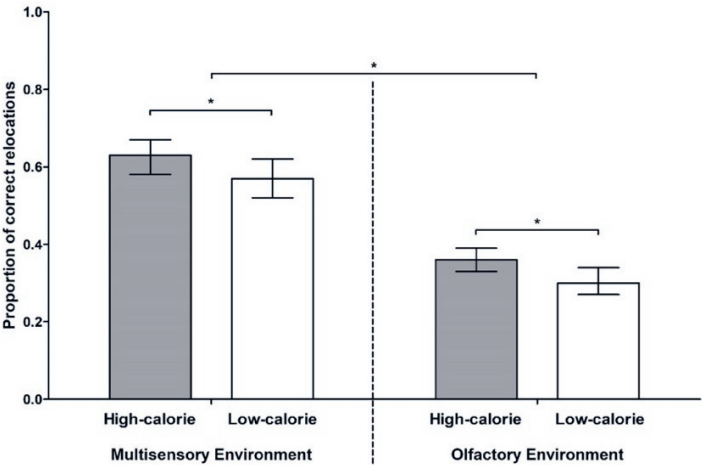


Figure 3.2. Food spatial memory accuracy. Human spatial memory for high-calorie and low-calorie food stimuli in two sensory environments, expressed as the proportion of correct food-to-pillar relocations. Error bars represent 95% confidence intervals.

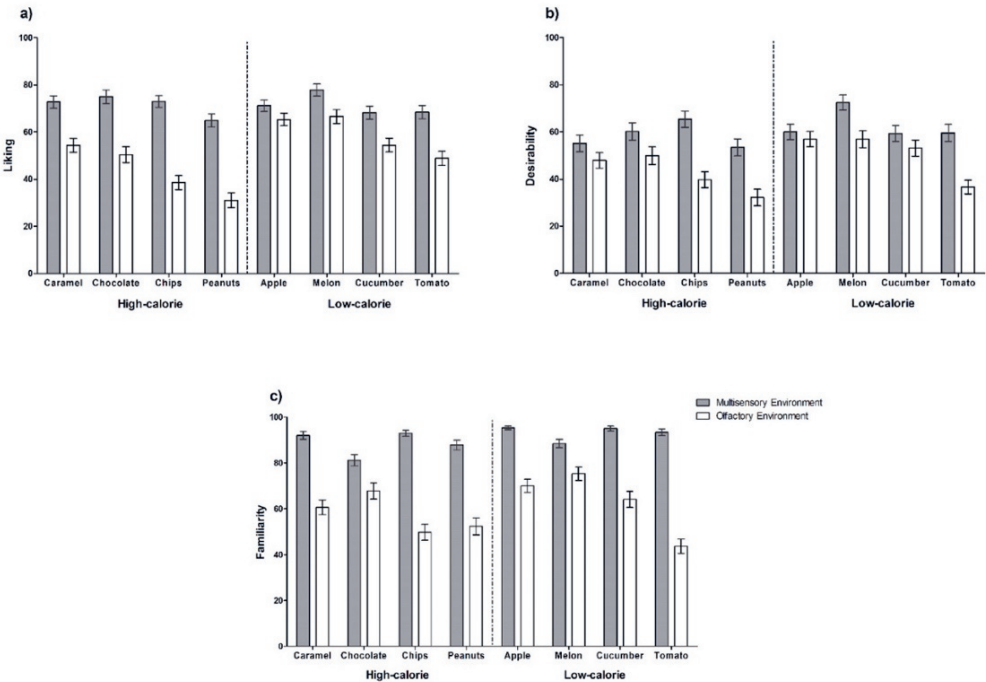


Figure 3.3. Food ratings across sensory environments. Liking (a), Desirability (b), and Familiarity (c) ratings (on a 100mm Visual Analogue Scale) for all food stimuli in the multisensory and olfactory environment. Error bars represent 95% confidence intervals.

Discussion

In a naturalistic multisensory experiment, individuals incidentally learned and more accurately recalled locations of high-calorie food stimuli. These results are compatible with the notion of “adaptive memory”, which contends that memory systems – much like other biological systems – were shaped by the forces of natural selection and should therefore show sensitivity to fitness-relevant content (Nairne, 2010; Nairne & Pandeirada, 2008b). Indeed, alternative interpretations of our findings that are grounded in more traditional memory frameworks, which champion the primacy of content-insensitive general learning mechanisms, can be ruled out by our data (Nairne, 2010). The possibility that the high-calorie spatial memory bias resulted from a greater “depth” of processing or motivational salience of high-calorie stimuli is minimal, given that we controlled for an individual’s personal familiarity with a food, as well as their explicit liking and desire to consume an item (Craik & Lockhart, 1972). In addition, high- and low-calorie food products were equivalent in their composition of important macronutrients (i.e. protein to carbohydrate and fat ratios), rendering it unlikely that differences in nutritional balance – rather than caloric content – is what drove the mnemonic advantage in the high-calorie condition (Simpson & Raubenheimer, 2005). However, the observation that (odor) familiarity predicted a higher frequency of overall correct relocations illustrates the importance of considering *both* content-sensitive and content-insensitive learning processes for human spatial cognition (de Vries *et al.*, 2020b).

Remarkably, the expression of the high-calorie bias in human spatial memory required only a limited presence of sensory information – granted that available sensory cues (such as odors) can communicate the relative value (e.g. caloric content) of potential foods – which further speaks to the processing efficiency of the mechanism (Schoener, 1971; Zoon *et al.*, 2016). We speculate that this could be due to an overlap in underlying (hippocampal) neural coding processes, despite variations in the (dominant) sensory modality used to explore the external world and significant objects contained within them (Schiller, 2015). For instance, it is feasible that hippocampal place cells show enhanced activity during recognition of objects (or cues) that flag a high-priority resource, independently of the type of sensory input received (Schiller, 2015). However, a sizeable difference in *overall* spatial memory performance was evident between sensory conditions, which may have resulted from a greater variety of sensory

information present in the multisensory environment. Individuals in the multisensory environment had a wider availability of sensory modalities (e.g. visual information) to utilize as spatial cues during encoding, which could have yielded a richer construction of mental spatial representations (Downs & Stea, 2011; Schifferstein et al., 2009). Going forward, research efforts would benefit from additionally documenting or matching participant samples on individual abilities to mentally represent and flexibly manipulate spatial information (i.e. between the viewer-centered perspective during navigation and the aerial map perspective during spatial recall) (Wolbers & Hegarty, 2010), for a more refined comparison of (food) location memory between sensory conditions.

In turn, differences in the expression of the high-calorie spatial memory bias may offer a novel explanation for why some individuals are less successful in maintaining a healthy energy balance within the modern food landscape (Allan & Allan, 2013). An enhanced memory for high-calorie food locations could make high-calorie options relatively easier to obtain within a diverse food environment, especially for those with a greater expression of the bias (Allan & Allan, 2013). In this manner, the cognitive bias may facilitate high-calorie food choice, by capitalizing on the tendency of individuals to prefer convenient easily-accessible items when making food decisions (Furst *et al.*, 1996). Similarly, it could stimulate individuals to visit calorie-laden food locations (e.g. fast food outlets) on a wider scale of space. Given the paucity of literature on the high-calorie spatial memory bias and its potential behavioral effects, further investigation is merited on what other cognitive processes are associated with the bias, and how it may influence the manner in which people navigate contemporary food replete settings.

Finally, our findings add to a growing literature that highlight the relevance of olfaction for eating behavior in humans, which is known to be the case across other species (Boesveldt & de Graaf, 2017; Jacobs, 2012). The human sense of smell is often depicted to be inferior to those of other mammals, such as dogs or rodents (McGann, 2017). However, our observations showcase the intact ability of individuals to distinguish different odor types, deduce caloric properties of signaled foods from odor cues, and localize odor objects in space (Jacobs, 2012; Wu *et al.*, 2020; Zoon *et al.*, 2016). Indeed,

a well-developed olfactory sense is thought to have conferred a survival advantage to (ancestral) hunter-gatherers (Bastir *et al.*, 2011; Majid & Kruspe, 2018).

Taken together, we find that human minds may continue to house an implicit cognitive system optimized for energy-efficient foraging within the fluctuating ancestral food environments in which memory evolved.

Materials and Methods

Participants. This experiment was part of the three-day Lowlands Science 2018 festival program (the Netherlands). A total of 512 attendees were analyzed: 258 participants (47% female; $M_{\text{Age}} = 28.2$ years, $SD = 9.1$; $M_{\text{BMI}} = 24.0$ kg/m², $SD = 3.6$) in the multisensory environment and 254 participants (50% female; $M_{\text{Age}} = 28.5$ years, $SD = 9.0$, $M_{\text{BMI}} = 23.8$ kg/m², $SD = 3.4$) in the olfactory environment. Data from 539 individuals were initially collected, but 21 files contained missing values and 6 files originated from individuals who participated in both sensory conditions which was an exclusion criterion. All participants (and/or their legal guardians) provided written informed consent prior to testing. This study was approved by the Social Sciences Ethics Committee of Wageningen University and was performed in accordance with relevant ethical guidelines and regulations. The hypothesis, full research protocol and analysis plan were preregistered, and can be accessed alongside reported data at <https://osf.io/2rwmt/>.

Spatial Memory Task. Participants were brought to a starting point within a room (area of 12 m²). They navigated between eight pillars at a fixed pre-determined order that was indicated by arrow signs on the floor. Although navigation schemes remained constant, the assignment of food stimuli to pillar locations (i.e. encoding order of caloric density - taste conditions) was randomized every hour and pillar frequencies did not differ between conditions. Participants tasted (or smelled) and provided ratings (i.e. liking, desire to eat, familiarity; **Figure 3.3**) on a food stimulus at all pillars. Participants then completed a surprise spatial memory task in a separate area. During recall, participants were randomly presented with a sequence of previous food stimuli and had to indicate the pillar location of each item on a (two-dimensional) digital map of the relevant room. The total number of possible pillar locations ($N = 8$) was displayed anew each recall round, and a pillar location could be selected more than once.

Food Stimuli. Four high-calorie ($M = 498.5$ kcal/100g, $SD = 35.8$) and low-calorie ($M = 34.3$ kcal/100g, $SD = 18.9$) food products and odor equivalents were used, with an equal number of sweet (e.g. High-calorie: chocolate brownie; Low-calorie: apple) and savory (e.g. High-calorie: potato chip; Low-calorie: cherry tomato) options for each. Food odors were matched on perceived intensity (i.e. 55-75 mm on a 100 mm Visual Analogue Scale) between caloric density - taste conditions and validated in previous research (de Vries *et al.*, 2020b). Food products were placed in bowls and refilled at regular time intervals to maintain a consistent presentation volume. Food odors were presented in (screw-capped) brown bottles (50 ml) containing scented cotton pads, which participants had to first open in order to smell. Odor bottles were also replaced regularly to uphold the desired odor intensity. All food stimuli were placed atop pillars and covered by identical cloches that participants had to open during navigation.

Statistical Analysis. For data from each sensory environment, a generalized linear mixed model (GLMM) with a random slope was formulated. A GLMM was chosen to flexibly model for correlated errors in the (non-normal) binary outcome variable (Bolker *et al.*, 2009), and linearity of covariates (on the logit scale) was shown to sufficiently capture their effects. The GLMM comprised fixed main and interaction effects for experimental factors *Caloric Density* and *Taste*, and random effects for the factor *Participant*. All effects were introduced on the logit scale. Additionally, in the fixed part of the model and also on the logit scale, *Gender*, *Age* (in tertiles), *Subjective SES*, *Food Allergies*, *Hunger* ratings, hours of *Sleep*, *Alertness*, *Alcohol consumption*, *Drug use*, *Smoking*, *Liking*, *Desirability*, and *Familiarity* were entered as covariates. Binary observations, conditional upon the random effects for participants, were assumed to follow a Bernoulli distribution. To test whether the type of sensory environment (i.e. multisensory versus olfactory) moderates food spatial memory accuracy and expression of the high-calorie bias, observations from both sensory rooms were combined into a single analysis, adding fixed main and interaction effects (e.g. with *Caloric Density*) of *Sensory Environment* to the GLMM. Ordinary likelihood ratio tests (using the -2LL test statistic) were used for testing, with p values derived from an approximation with the chi-square distribution. Inference was based on Laplacian integration employing the *lme4* package from R (Bates *et al.*, 2019). Detailed

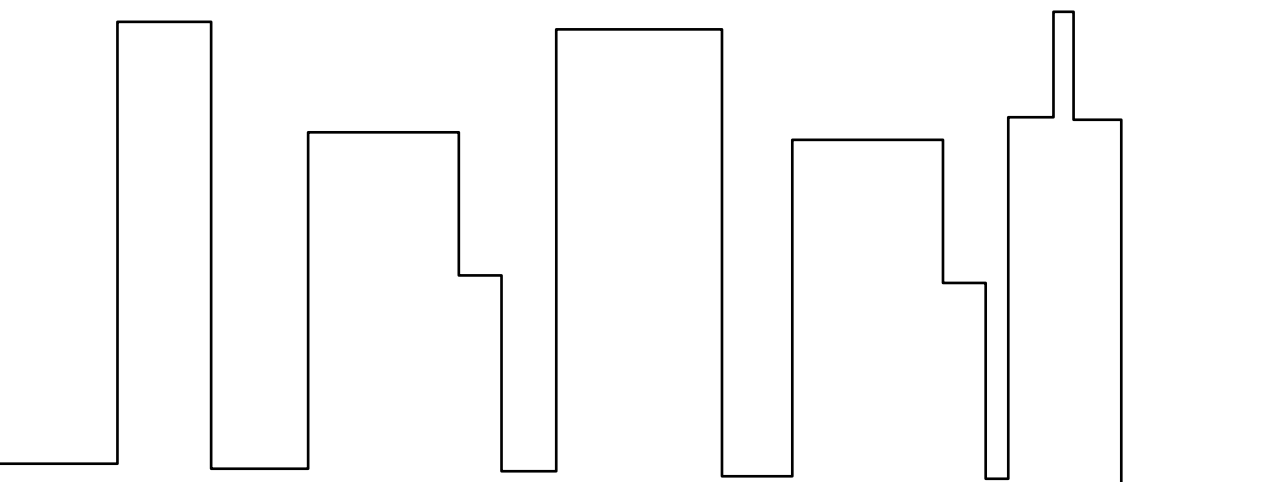
information on the measurement of covariates and the model selection process can be found at <https://osf.io/2rwmt/>.

Data Availability

The data that support the findings of this study are available on the Open Science Framework repository with the identifier DOI 10.17605/OSF.IO/2RWMT.

Acknowledgments

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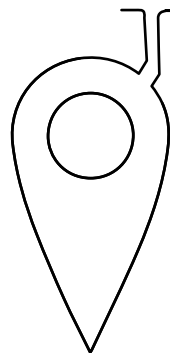
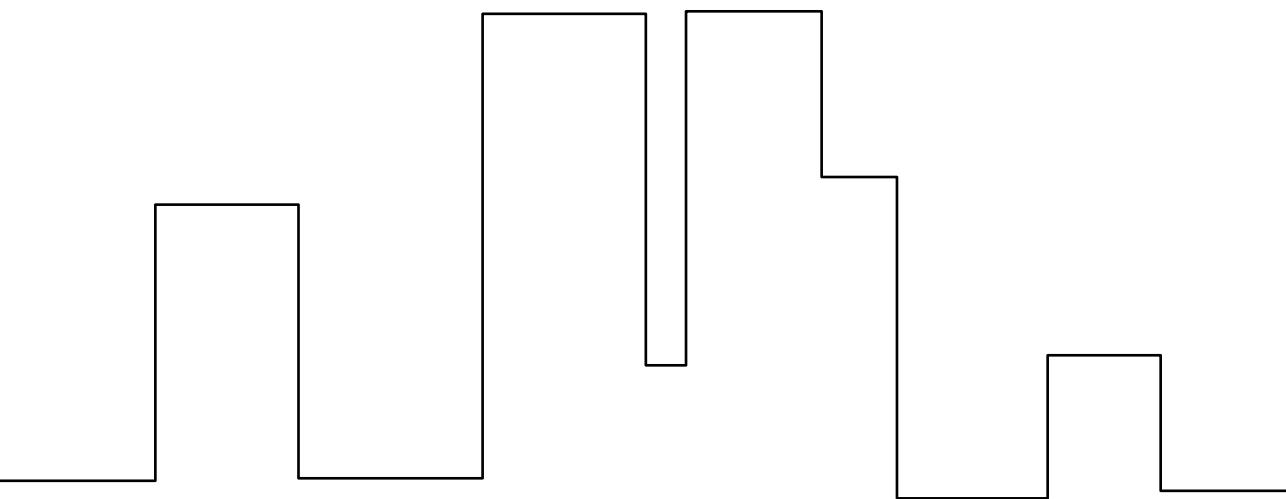
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Chapter 4

Locating calories:

Does the high-calorie bias
in human spatial memory
influence how we navigate
the modern food environment?

Abstract

Human memory appears to be adaptively “biased” towards remembering the locations of (fitness-relevant) high-calorie nutritional resources. It remains to be investigated whether this high-calorie bias in human spatial memory influences how individuals navigate the modern food environment, and whether it is proximally associated with attentional processes. 60 individuals completed computer-based food eye-tracking and spatial memory tasks in a lab setting, as well as a food search and covert food choice task in an unfamiliar supermarket. The high-calorie spatial memory bias was replicated, as individuals more accurately recalled locations of high-calorie relative to low-calorie foods, regardless of hedonic evaluations or familiarity with foods. Although individuals were faster at (re)locating high-calorie (versus low-calorie) items in the supermarket, the bias did not predict a lower search time for high-calorie foods, or a higher proportion of high-calorie food choice. Rather, an enhanced memory for high-calorie food locations was associated with a lower perceived difficulty (i.e. greater ease) of finding high-calorie items in the supermarket, which may potentiate later choice of a high-calorie food. The high-calorie spatial memory bias was also found to be expressed independently of the amount of visual attention individuals allocated to high-calorie versus low-calorie foods. Findings further substantiate the notion that human spatial memory shows sensitivity to the caloric content of a potential resource and automatically prioritizes those with greater energy payoffs. Such a spatial mechanism that was adaptive for energy-efficient foraging within fluctuating ancestral food environments could presently yield maladaptive “obesogenic” consequences, through altering perceptions of food search convenience.

General Introduction

A growing body of evidence proposes that the human mind was functionally shaped by evolutionary selection pressures to maximize fitness, much like physical traits were (Tooby & Cosmides, 1992; Tooby & Cosmides, 2005). That is, our present cognitive architecture is thought to harbour inbuilt mechanisms that were optimized for solving specific fitness-relevant “adaptive” problems encountered within the ancestral environments in which we evolved (Tooby & Cosmides, 1992; Tooby & Cosmides, 2005). One such cognitive mechanism that could have evolved as an adaptation for foraging within harsh ancestral food settings is a prioritization (or bias) in human memory for the locations of high-calorie foods (Allan & Allan, 2013; New *et al.*, 2007b; de Vries *et al.*, 2020a; de Vries *et al.*, 2020b). Indeed, a comparable foraging-related cognitive mechanism has been documented in various (non-human) primate species (Cunningham & Janson, 2007; Janmaat *et al.*, 2014; Janson, 1998). However, empirical research on the existence of such a “high-calorie bias” in human spatial memory, and particularly whether (or in what manner) it influences how individuals navigate the modern obesogenic food environment, is currently limited.

A recurring adaptive problem faced by all species is the efficient attainment of nutritional resources (Schoener, 1971). For a substantial portion of human evolutionary history, the acquisition of food was characterized by extensive hunting-gathering activities within a fluctuating landscape, where food supply varied along both temporal and spatial dimensions (Adler *et al.*, 2006; Stiner & Bar-Yosef, 2005; Stiner & Kuhn, 2009). The survival and reproductive success of an individual were therefore a function of the energy-efficiency of foraging bouts, such as the fluency with which a forager could identify and (re)locate high-quality resources, as they became available or valuable over time (MacArthur & Pianka, 1966; Schoener, 1971). It follows that a cognitive adaptation that could have evolved to support energy-efficient foraging, is one that automatically assesses the profitability of potential food resources and prioritizes the locations in memory of those higher in caloric quality (Krasnow *et al.*, 2011; New *et al.*, 2007b; de Vries *et al.*, 2020a; de Vries *et al.*, 2020b). In a series of recent investigations, we obtained evidence consistent with the existence of such an implicit high-calorie bias in human spatial memory for foods: Across sensory modalities (e.g. vision and olfaction) and experimental paradigms, we found that individuals more accurately recalled locations of high-calorie (relative to low-calorie) food stimuli –

independently of hedonic food evaluations, personal familiarity with foods, encoding time, or encoding conditions (i.e. incidental versus intentional learning) (de Vries *et al.*, 2020a; de Vries *et al.*, 2020b).

If human spatial memory is indeed attuned to optimal foraging within erratic ancestral food habitats, this begs the question of what the behavioral implications of the high-calorie spatial memory bias are within a modern (food abundant) foraging context. The (once adaptive) high-calorie bias in spatial memory may presently confer maladaptive obesogenic effects, by directly enhancing the ease with which high-calorie items are located and acquired within a heterogeneous food environment (Allan & Allan, 2013; de Vries *et al.*, 2020b). However, the evidence is currently inconclusive: Allan & Allan (2013) observed that an improved location memory for high-calorie snack foods (relative to low-calorie fruits and vegetables) predicted a greater BMI in women. De Vries *et al.* (2020b) similarly reasoned that the high-calorie spatial memory bias may promote unhealthy high-calorie food choice, but did not find any systematic relationships between the expression of the cognitive bias and eating-related parameters. Given that previous efforts were limited to either distal (anthropometric) markers of dietary intake or controlled food choice measures in lab settings, finer-grained effects of the high-calorie spatial memory bias on an individual's eating behavior could have gone undetected. Therefore, the current study represents a more powerful and ecologically valid test of the potential behavioral implications of a high-calorie bias in human spatial memory, by examining its relation to proximate foraging-related outcomes (i.e. food search and food choice) within a real-world food environment.

Similarly, it remains to be elucidated what processes are proximally associated with the high-calorie bias in human spatial memory, as evolved cognitive mechanisms often have a neurophysiological basis (Cosmides & Tooby, 1997). These insights would be especially relevant for health interventions aiming to directly alter the expression of the bias. With regards to candidate proximal mechanisms, it is reasonable to expect that a bias in attention for high-calorie (relative to low-calorie) food cues may facilitate an enhanced memory for locations of high-calorie foods. Namely, evidence has accumulated for the phenomenon of "object-based spatial attention", in which individuals make use of objects to guide attentional processing to specific locations in the visual field, such as the spatial region an object occupies (Arrington *et al.*, 2000). As

such, one can assume that a greater attentional allocation to high-calorie foods could similarly lead to an enhanced attentional processing of (and later superior memory for) the locations of those items. An additional justification stems from research suggesting that high BMI (overweight/obese) individuals display a visual attention bias for high-calorie foods, and the magnitude of the high-calorie spatial memory bias has been previously linked to a higher BMI (Allan & Allan, 2013; Castellanos *et al.*, 2009; Hendrikse *et al.*, 2015; Werthmann *et al.*, 2011). Indeed, spatial memory performance for gatherable foods (e.g. fruit) has been shown to improve with the amount of attention deployed to them, particularly in situations of “item-specific” motivation (i.e. when a forager encounters a valuable high-calorie gatherable resource; Krasnow *et al.*, 2011). Direct examination of the relationship between food-related attention biases and the high-calorie spatial memory bias is thus warranted, especially in light of the fact that associations between attention and (episodic) memory faculties vary depending on the exact information that is attended to and later recalled (e.g. Allan *et al.*, 2012; Becker *et al.*, 2005).

In sum, the aim of the present study was twofold. Our primary research objective was to investigate the potential implications of a high-calorie bias in human spatial memory on the food search and food choice of individuals navigating a real-world food environment. Secondly, we examined the extent to which high-calorie biases in visual attention are related to the high-calorie bias in spatial memory. We hypothesized the following outcomes:

H_{1A} : The high-calorie bias in spatial memory predicts a faster localization of (i.e. lower search time for) high-calorie relative to low-calorie foods.

H_{1B} : The high-calorie bias in spatial memory predicts a higher proportion of high-calorie food choice.

H_2 : An attention bias for high-calorie foods will be positively associated with the high-calorie spatial memory bias.

Methodology

Design

The study had a repeated measures design with *Caloric Density* (High versus Low) as a within-subjects factor. Each participant completed a series of lab-based computer tasks (i.e. eye-tracking and spatial memory tasks) and a supermarket-based

food search and (covert) food choice task in two test sessions separated by a delay of at least one day. The hypotheses, experimental design, and data analysis plan were preregistered and are available with study data on the Open Science Framework database (Project URL: <https://osf.io/7hmf/>).

Participants

60 healthy university students (73% female; $M_{\text{Age}} = 24.6$ years, $SD = 3.2$) took part in the research. The majority of participants had a Caucasian background (82% Caucasian; 8% Asian; 8% Latino; 2% Other) and were postgraduate students (80% postgraduates; 20% undergraduates). The sample size was determined *a priori* via a power calculation on our primary research objective (see pre-registration link). Participants were limited to the BMI range of 18.5 – 30 kg/m² ($M = 22.8$ kg/m², $SD = 2.4$), to minimize ceiling effects (for BMI values > 30 kg/m²) and floor effects (for BMI values < 18.5 kg/m²) on food-related attention bias measures (Castellanos *et al.*, 2009; Giel *et al.*, 2011). Moreover, we included only individuals who were sufficiently *unfamiliar* with the test supermarket environment (i.e. did not habitually grocery shop there, did not visit the supermarket in the month before testing, and self-reported a store familiarity score lower than 50mm on a VAS ranging from 0 ("Not At All") to 100 ("Very Much") mm), in order to circumvent potential ceiling effects on food search performance (O'Neill, 1992). Finally, individuals were not included when reporting a dietary restriction to specific foods (e.g. meat), a medical history of eating or psychiatric disorders, or participation in previous related studies. All participants provided written informed consent prior to testing and were financially compensated. This study received ethical approval from the Social Sciences Ethics Committee of Wageningen University.

Apparatus and Stimuli

Food stimuli in computer tasks. Standardized images of (sweet/savory) high- and low- calorie foods were obtained from the *Food Pics* database (Blechert *et al.*, 2014). High-calorie items were defined as those that contained at least 225 – and low-calorie items at most 60 – kcal per 100 grams of food (de Bruijn *et al.*, 2017; World Cancer Research Fund/American Institute for Cancer Research, 2007). For the spatial memory task, a set of 12 (unbranded) food pictures was chosen for each caloric density group, encompassing fruits and vegetables for the low-calorie condition, and baked and fried goods as high-calorie variants (de Vries *et al.*, 2020b). For the eye-tracking task, a subset of 10 high- and low-calorie food stimuli from that of the spatial memory

task was used (see *Food Pics Catalogue Numbers* in the Supplemental Material (**Appendix Chapter 4**)). Importantly, an equal number of taste (i.e. sweet and savory) options were included across caloric density categories, as working and spatial memory faculties are documented to process tastes differently (Meule *et al.*, 2012a; de Vries *et al.*, 2020b).

In both tasks, high- and low-calorie images differed on caloric density, total energy content, perceived caloric content, and perceived healthiness (see **Table A4.1** in the Supplemental Material). Furthermore, high- and low-calorie stimuli were matched on nutrient balance (i.e. protein to carbohydrate and fat ratios; Simpson *et al.*, 2003), pertinent image characteristics (e.g. color, size, brightness), recognizability, and subjective complexity ratings (see **Table A4.1**) (Graham *et al.*, 2011; Werthmann *et al.*, 2011).

Free-viewing eye-tracking task. The eye-tracking paradigm was adapted from Graham *et al.* (2011) and Werthmann *et al.* (2011). The task was created with Tobii Pro Lab (Tobii Technology, Danderyd, Sweden) and run on a Windows laptop (screen size: 15.6 inches; resolution: 1920 x 1080) with a Tobii X2-60 eye-tracker mounted on the computer screen. Participants were seated approximately 65 centimeters away from the screen and placed their heads on a chin-rest. A five-point calibration procedure was conducted prior to recording.

The eye-tracking task comprised a total of 120 trials: 80 critical trials and 40 filler trials. Critical trials consisted of 20 high- and low-calorie food image pairs, and each pair was presented four times. High- and low-calorie foods occurred equally frequently on the left and right sides of an image pair. Filler trials consisted of 10 pairs of non-food images (e.g. tools and office supplies), each also presented four times. All trials began with a central fixation cross that was displayed for 2000 milliseconds, whereas trials were shown for 3000 milliseconds. During recording, participants were instructed to look at presented images freely – as if they were watching television – and to focus on the fixation cross displayed between trials. The order of critical and filler trials was randomized differently for each participant.

Unknown to participants, the computer screen was divided into a left, middle, and right Area of Interest [AOI]. Only visual fixations – defined as eye movements that are maintained for at least 100 milliseconds – directed to the left or right AOI during critical trials were extracted for further analyses (Werthmann *et al.*, 2011).

Spatial memory task. The spatial memory task was previously validated as an instrument to measure food location memory accuracy in the target population (Allan & Allan, 2013; de Vries *et al.*, 2020b). The task was run on E-Prime 2.0 using computers standardized across screen size (19.3 inches) and resolution (1280 x 1024). Participants were asked to imagine that an international food market with 24 food stalls was taking place on a (unfamiliar) university campus. Participants were then shown 12 images of either high-calorie foods or low-calorie alternatives, followed by an image of a university campus map showcasing all possible stall locations (N=24), at a duration of three seconds each. After, the location of the stall selling each food item (N=12) was indicated one-by-one on the campus map by a green crosshair. During the location viewing process, participants were instructed to rate each food item on desirability and familiarity. Following a two-minute break, participants completed a series of 12 spatial memory tests in which they were randomly presented with one of the previous food images and required to specify (via mouse-click) its correct corresponding stall location on the campus map. The total number of possible stall sites was displayed anew each recall round, and a stall location could be selected more than once although assigned locations did not overlap between foods. The order of stimulus presentation and the stimuli itself (i.e. food-location pairs) were randomized differently for each participant. Furthermore, the order in which participants performed the spatial memory task between caloric density conditions was counterbalanced.

Food search task. The food search task was carried out using EyeQuestion software (Logic8 B.V., Elst, Gelderland, the Netherlands). A set of 16 food products (N=8 per caloric density group) sold at the test supermarket (i.e. *Jumbo Verberne Wageningen*) was selected for the task. Chosen high- and low-calorie products (e.g. High-calorie: Chocolate cookies and Potato chips; Low-calorie: Oranges and Eggplant; see **Table A4.2** in the Supplemental Material) had an equal number of sweet and savory items, were matched on spatial distributions within the supermarket (i.e. floor sections and vertical height) as closely as possible, and were piloted to verify correct caloric content and healthiness perceptions.

For the encoding phase of the task, participants were first walked through all supermarket aisles by the experimenter and instructed to observe their surroundings as they moved. The order in which supermarket aisles were explored was counterbalanced across participants, ensuring that (target) high- and low-calorie aisles were encountered

equally often at the beginning and end of a walking sequence. Individuals were then provided with a tablet and presented with a sequence of images of target food products, which they had to (re)locate as quickly as possible within the supermarket. Upon finding a product, participants had to rate how difficult it was to find, product familiarity, and product attractiveness. Participants also had to rate how eye-catching they found the respective product aisle, before proceeding on to the next food item. The presentation order of food products during the search (recall) portion of the task was randomized differently per participant.

Procedure

Participants were informed that the experiment aimed to investigate how people perceive and (cognitively) process foods typically found in the modern food environment. They were also told that they would be rewarded with paid-for groceries at the end of the study as part of their compensation. Hunger states were standardized before sessions by instructing individuals to consume their habitual meals or snacks no later than two hours – and no sooner than 45 minutes – before testing. Test sessions were scheduled around typical breakfast and lunch times to facilitate compliance to pre-testing requirements, as well as outside of peak supermarket hours to ensure relatively calm surroundings for the food search task.

For the first test session in the lab, participants were seated in isolated testing booths fitted with a computer. Data on demographics and hunger state were first recorded via a questionnaire. Participants then had to complete the free-viewing eye-tracking task. Following a brief intermission, participants performed the spatial memory task for both caloric density conditions: Individuals were first exposed to a practice trial involving the encoding and recall of (non-food) object locations to familiarize themselves with the protocol. After, they completed the actual spatial memory task with (high- and low-calorie) food images, with a five-minute break between conditions. Upon finishing, participants answered questions on healthy eating goals. The first test session took approximately 60 minutes (**Figure 4.1**).

At least one day later, participants arrived at the test supermarket. After providing preliminary ratings (i.e. Hunger), participants performed the food search task and rated their general sense-of-direction upon completion. As part of the covert food choice measure, they were then given a budget of 10 euros and 10 minutes to freely

shop for food items within the supermarket, the receipts of which were handed over to the experimenter. The second test session took an average of 30 minutes (**Figure 4.1**).

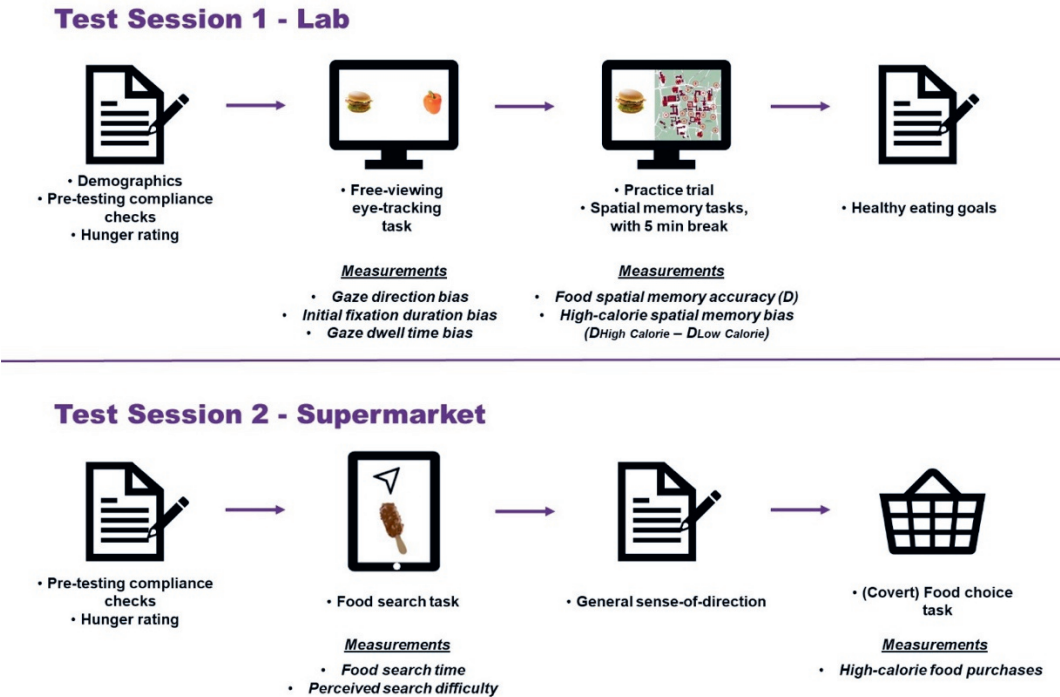


Figure 4.1. Experimental procedure. Participants completed a series of tasks in a lab and (unfamiliar) supermarket setting, on two separate occasions.

Measurements

Primary outcome variables. Food search performance was operationalized as the time (in seconds) required to (re)locate a target food product in the food search task, from the onset of stimulus presentation. Perceived search performance was also gauged by asking participants to rate how difficult it was to find a food product on a 100mm VAS (anchored from “Not At All” to “Very Much”), as an alternative to (objective) search time. A similar (subjective performance) VAS scale was employed in earlier studies and shown to accurately covary with individuals’ actual task performance (de Vries *et al.*, 2020b). Search times and difficulty ratings were averaged per caloric density category.

The number of high-calorie food products bought from the (rewarded) groceries of each participant, expressed as a proportion of the total number of purchased food items, was taken as a covert measure of high-calorie food choice.

Predictor variables. Spatial memory accuracy for high- and low-calorie foods was calculated as the average ‘pointing error’ or Euclidian distance (D) between true and indicated stall locations of each food type (cf. Allan & Allan, 2013; de Vries *et al.*, 2020b). Consequently, lower D scores denote a higher accuracy in food spatial memory. The difference in spatial memory accuracy for high- and low-calorie foods ($D_{\text{High Calorie}} - D_{\text{Low Calorie}}$) was taken to represent the high-calorie bias in spatial memory. Accordingly, negative values indicate an enhanced spatial memory for high-calorie foods.

Three eye movement metrics that reflect different temporal components of attention were measured to directly assess attention biases for high-calorie foods (Castellanos *et al.*, 2009; Graham *et al.*, 2011; Werthmann *et al.*, 2011):

The gaze direction bias is an index of biases in initial attentional orientation. It was calculated as the number of critical trials in which the first fixation was directed to a high-calorie food, as a proportion of the total number of critical trials in which first fixations were observed. A proportion higher than 0.5 indicates an orientation bias towards high-calorie foods; a proportion lower than 0.5 indicates an orientation bias towards low-calorie foods.

The initial fixation duration bias is a proxy for biases in early attentional maintenance. It represents the duration of the first fixation directed to a particular image type (i.e. the first fixation to occur on an image following the onset of a critical trial), and was calculated as the difference between the average duration of initial fixations on

high- and low-calorie foods (across all critical trials per participant). A positive score denotes a longer initial attentional maintenance on high- versus low-calorie foods.

The gaze dwell time bias is informative of biases in maintained attention. It was calculated by subtracting the average fixation time (i.e. using the sum of individual fixations across critical trials) on low-calorie food images from the average fixation time on high-calorie food images. A positive score suggests a longer maintained attention on high-calorie foods.

At the conclusion of testing, eye movements were detected on an average of 98.9% of critical trials and all participants had sufficient fixation data recorded (i.e. at least 80% of critical trials). Gaze direction bias scores were not found to correlate with either initial fixation duration ($r_s = .04$), $p = .757$, or gaze dwell time bias measures ($r_s = 0.19$), $p = .152$. Similarly, the (relative) amount of time individuals initially fixated on high-calorie food items did not correlate with the overall time individuals fixated on high-calorie versus low-calorie food images ($r_s = 0.12$), $p = .359$, suggesting that the three bias scores indeed reflect different underlying components of visual attention.

Control measures. To eliminate confounding influences of food ‘wanting’ on spatial memory accuracy, we required participants to rate a food item’s Desirability on a 100mm VAS (anchored from “Not At All” to “Very Much”) in the spatial memory task (de Vries *et al.*, 2020a; de Vries *et al.*, 2020b). Furthermore, individual exposure to a food type was documented using a five-item Familiarity scale (Tuorila *et al.*, 2001) in both spatial memory and food search tasks. Choice options of the Familiarity scale reflect behaviorally-meaningful differences relevant to individual experiences with a food (e.g. having tasted versus not tasted a specific item; Tuorila *et al.*, 2001), and both Desirability and Familiarity measures were shown to effectively capture additional variation in spatial memory performance not attributable to a food’s nutritional properties (de Vries *et al.*, 2020a; de Vries *et al.*, 2020b).

To specifically control for extraneous effects on food search performance, we required participants to record the Attractiveness of (target) food products, how Eye-catching a product aisle was, and Familiarity with the test supermarket on a 100mm VAS (anchored from “Not At All” to “Very Much”). We adopted a “continuous” VAS format for these controls, as opposed to an “ordinal” forced-choice alternative such as a Likert scale, to better detect subtle deviations in these measures between individuals and respective products (McCormack *et al.*, 1988). Individuals were additionally asked

to quantify their General Sense-of-Direction on a seven-point scale ranging from "Poor" to "Good", as self-reports of this measure are shown to correlate with field measures of navigational ability in unfamiliar environments (Kozlowski & Bryant, 1977; New *et al.*, 2007b).

As an individual's explicit nutritional intentions were found to significantly predict eating behavior in previous studies (de Vries *et al.*, 2020b), a Healthy Eating Goals measure was administered with two items (*In my daily life, I strive to eat healthy, It is important to me to eat healthy foods*) rated on a seven-point scale anchored from "Strongly Disagree" to "Strongly Agree" (de Vries *et al.*, 2020b). Finally, demographic characteristics (e.g. *Sex, Age, Ethnicity*) and *Hunger* states (100mm VAS anchored from "Not At All" to "Very Much") at the onset of each test session were recorded.

Data Analysis

Data were analyzed using IBM SPSS Statistics 25 with statistical significance defined as $p < .05$. The first statistical analysis was of an exploratory nature, in order to firstly confirm the existence of the high-calorie bias in human spatial memory prior to assessing its behavioral and attentional correlates. Remaining statistical models represent confirmatory analyses that correspond to our preregistered hypotheses.

Caloric Density and Spatial Memory Accuracy (Exploratory). To explore whether human spatial memory is indeed biased for high-calorie foods, we formulated a random intercept linear mixed model with main and interaction effects of *Caloric Density* and *Taste* as fixed factors, *Participant* as random factor (covariance structure: Variance Components), *Sex, Age, Ethnicity, Caloric Density Order, Desirability, Familiarity*, and *Hunger* as covariates, and *Spatial Memory Accuracy (D)* as the dependent variable. The model selection process involved a backward stepwise approach: Fixed effects of the saturated model (above) were finalized based on Maximum Likelihood (ML) ordinary likelihood ratio tests using the -2 log likelihood (-2LL) test statistic between nested models. Model selection was made on the basis of parsimony and the final model (with *Caloric Density, Taste*, and *Desirability*) was refitted with REML estimations.

High-calorie Spatial Memory Bias and Food Search (H_{1A}). To determine whether the high-calorie bias in spatial memory predicts a faster localization of high-calorie foods, we formulated a multiple linear regression model ($N=1$; simultaneous entry method) with *Search time for high- versus low-calorie foods* ($\text{Time}_{\text{High-calorie}} - \text{Time}_{\text{Low-calorie}}$) as the dependent variable.

Low-calorie) as the dependent variable and demographics (i.e. *Sex, Age, Ethnicity*), *Hunger* ratings at encoding, *Encoding (Walking) order*, *General Sense-of-Direction*, *Familiarity with the supermarket*, *Familiarity with high- versus low-calorie foods*, *Attractiveness of high- versus low-calorie foods*, *Eye-catching ratings of high- versus low-calorie food aisles*, and the *High-calorie spatial memory bias* ($D_{\text{High Calorie}} - D_{\text{Low Calorie}}$) as predictor variables.

High-calorie Spatial Memory Bias and High-calorie Food Choice (H_{1B}).

To test whether the high-calorie bias in spatial memory predicts prospective high-calorie food purchases, we performed a multiple linear regression analysis (N=1; simultaneous entry method) on *High-calorie food choice* with demographics (i.e. *Sex, Age, Ethnicity*), *Hunger* ratings at encoding, *Familiarity with high- versus low-calorie foods*, *Attractiveness of high- versus low-calorie foods*, *Eye-catching ratings of high- versus low-calorie product aisles*, *Healthy Eating Goals*, and the *High-calorie spatial memory bias* ($D_{\text{High Calorie}} - D_{\text{Low Calorie}}$) as predictor variables.

Attention Bias for High-calorie Foods and the High-calorie Spatial Memory Bias (H₂). To determine whether biases in attention towards high-calorie foods covary with the expression of the high-calorie spatial memory bias, we regressed (N=1; simultaneous entry method) the *High-calorie spatial memory bias* ($D_{\text{High Calorie}} - D_{\text{Low Calorie}}$) on demographics (i.e. *Sex, Age, Ethnicity*), *Spatial memory task order*, *Hunger* ratings at encoding, *Desirability of high- versus low-calorie foods*, *Familiarity with high- versus low-calorie foods*, *Gaze direction bias*, *Initial fixation duration bias*, and *Gaze dwell time bias*.

Results

The high-calorie bias in human spatial memory was replicated.

In the lab-based spatial memory task, the average accuracy in food spatial memory across caloric density conditions was 155.92 ($SD = 151.03$) pixels. Individuals demonstrated a more accurate memory (i.e. smaller pointing error or D) for locations of high-calorie foods compared to that of low-calorie alternatives, $F(1,1380) = 9.23$, $p = .002$, $\eta^2 = 0.007$, 90% CI $\eta^2 [0.001, 0.02]$ (**Figure 4.2A**). In addition, a significant main effect of Taste on spatial memory accuracy was observed, with individuals better recalling locations of savory (as opposed to sweet) tasting stimuli, $F(1,1384) = 7.90$, $p = .005$, $\eta^2 = 0.006$, 90% CI $\eta^2 [0.001, 0.01]$ (**Figure 4.2B**), indicating the expression of high-calorie and savory-taste biases in human spatial memory, respectively. These

effects occurred regardless of demographics (e.g. Sex), hedonic evaluations, or reported familiarity with foods. Similarly, post-hoc analysis revealed that the time participants took to encode food locations did not influence spatial memory performance $F(1,1399) = 0.38$, $p = .540$, or attenuate either the high-calorie or savory-taste bias in human spatial memory. Finally, food spatial memory accuracy improved with a higher rated desire to eat a food ($B = -0.49$, 95% CI = $[-0.75, -0.23]$), $F(1,1405) = 13.52$, $p < .001$, $\eta^2 = 0.01$, 90% CI η^2 $[0.003, 0.02]$.

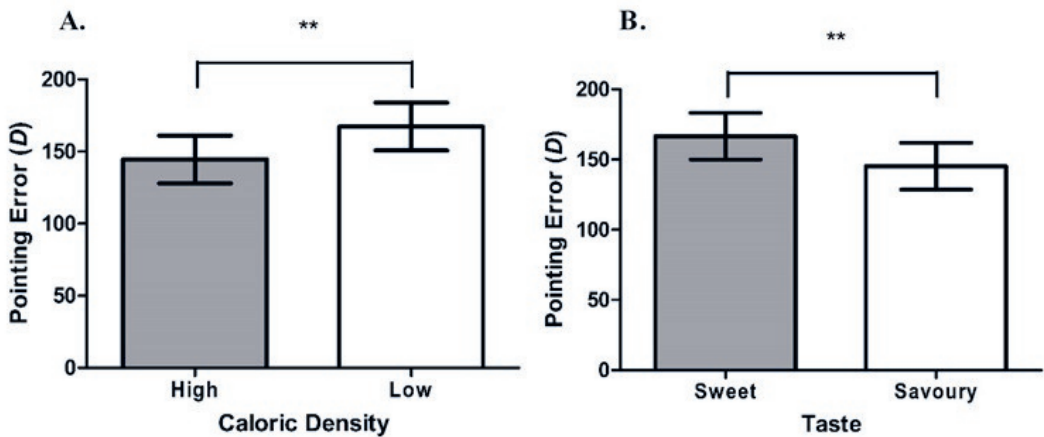


Figure 4.2. Spatial memory accuracy for (A) Caloric Density and (B) Taste food groups, measured as the “pointing error” (D in pixels) between true and indicated food locations. Lower values indicate a lower pointing error and higher accuracy in food spatial memory. A double asterisk indicates a significant difference with $p < .01$. Error bars represent 95% confidence intervals.

The high-calorie bias in spatial memory did not predict food search time, but a lower perceived search difficulty for high-calorie foods.

With regard to the food search task, individuals were moderately faster at (re)locating high-calorie than low-calorie target food products within the unfamiliar supermarket (47.6 vs 54.1 seconds; **Table A4.3**), Mean search time difference $\text{High-Low calorie} = -6.48$ seconds, 95% CI = $[-12.54, -0.43]$, $t(59) = -2.14$, $p = .036$, $d = 0.35$. Upon closer inspection, follow-up (linear mixed model) analysis showed a significant Caloric Density and Taste interaction, $F(1,900) = 8.96$, $p = .003$, $\eta^2 = 0.01$, 90% CI η^2 $[0.002, 0.02]$. The high-calorie advantage in search time was found only for savory products, in which high-calorie - savory items had 9.40% lower search times compared to low-calorie - savory counterparts (95% CI = $[3.40, 15.40]$), $p = .002$. Perceived search difficulty followed search time results closely ($r_s(954) = .640$, $p < .001$; **Table A4.3**),

with follow-up (linear mixed model) analysis similarly yielding a significant Caloric Density and Taste interaction, $F(1,872) = 6.97$, $p = .008$, $\eta^2 = 0.01$, 90% CI η^2 [0.001,0.02], owing to a 9.70% lower rated difficulty of finding high-calorie - savory (compared to low-calorie - savory) items (95% CI = [2.40, 17.10]), $p = .010$.

However, the high-calorie spatial memory bias did not predict the faster localization of high-calorie foods in the supermarket ($B = 0.04$, 95% CI = [-0.06,0.14]), $t(48) = 0.75$, $p = .228$. Exploratory analysis revealed the high-calorie bias in spatial memory was instead predictive of a lower perceived difficulty (i.e. greater ease) of finding high-calorie relative to low-calorie products ($B = 0.04$, 95% CI = [0.002,0.09]), $t(56) = 2.12$, $p = .039$ (**Table 4.1**).

Table 4.1.

Predicting the perceived difficulty of finding high-calorie versus low-calorie food products in an unfamiliar supermarket environment from the high-calorie bias in spatial memory.

Variable	B	95% CI	Beta	<i>t</i>	<i>p</i>	R	R ²
Model 1^a							
Constant	-3.33	-6.21 – -0.47		-2.33	.024*	.422	.178
Eye-Catching High – Low Calorie	-0.41	-0.64 – -0.18	-0.42	-3.54	<.001***		
Model 2							
Constant	-2.58	-5.5 – 0.35		-1.77	.083	.475	.226
Eye-Catching High – Low Calorie	-0.42	-0.65 – -0.20	-0.44	-3.76	<.001***		
High-calorie Spatial Memory Bias ^b	0.04	-0.003 – 0.08	0.22	1.88	.066		
Model 3							
Constant	-2.37	-5.23 – 0.50		-1.66	.103	.526	.276
Eye-Catching High – Low Calorie	-0.49	-0.71 – -0.26	-0.51	-4.25	<.001***		
High-calorie Spatial Memory Bias ^b	0.04	0.002 – 0.09	0.24	2.12	.039*		
Attractiveness High – Low Calorie	0.24	-0.002 – 0.48	0.24	1.98	.052		

^aFrom a stepwise regression analysis, with sex, age, ethnicity, hunger ratings, encoding (walking) order, general sense-of-direction, familiarity with the supermarket, familiarity with high- versus low-calorie foods, attractiveness of high- versus low-calorie foods, and eye-catching ratings of high- versus low-calorie food aisles entered as covariates.

^b $D_{\text{High Calorie}} - D_{\text{Low Calorie}}$ (Lower values denote a greater bias in spatial memory for high-calorie foods)

* $p < .05$; ** $p < .01$; *** $p < .001$

The high-calorie bias in spatial memory did not predict high-calorie food choice.

Across participants, high-calorie food choices accounted for 47% (range: 0 – 100%) of all groceries purchased. The average caloric density of chosen foods was 230.18 ($SD = 106.87$) kcal/100g. Contrary to expectations, the high-calorie spatial memory bias did not affect the proportion of high-calorie food products individuals purchased ($B = -6.75 \times 10^{-5}$, 95% CI = [-0.001, 0.001]), $t(50) = -0.12$, $p = .453$. As exploratory tests, we alternatively operationalized high-calorie food choice as the proportion of total costs an individual spent on high-calorie food products, as well as the average caloric density of groceries chosen. However, the high-calorie spatial memory bias was not significantly associated with either outcome (both p 's > .05; **Table A4.4**).

In light of the prior finding that the high-calorie spatial memory bias covaried with the reported difficulty of finding high-calorie (versus low-calorie) products, a corresponding analysis was conducted to explore the relationship between perceived search difficulty and prospective high-calorie food choice. A trend was found for a negative correlation between the perceived difficulty of finding high-calorie products and the proportion of high-calorie foods purchased ($r_s(60) = -0.25$), $p = .058$, whereas no association between prospective high-calorie food choice and objective search time for high-calorie foods was observed ($r_s(60) = -0.06$), $p = .655$.

The high-calorie spatial memory bias was not associated with a bias in visual attention for high-calorie foods.

Individuals displayed an average gaze direction bias score of 0.51 ($SD = 0.06$), which did not significantly differ from chance level, $t(59) = 1.12$, $p = .269$, indicating an equal initial attention orientation towards high- and low-calorie food stimuli. Regarding early attention maintenance, participants initially fixated on high-calorie items for a duration of 250.88 milliseconds (versus 239.16 milliseconds on low-calorie counterparts), although the high-calorie bias in initial fixation duration did not reach statistical significance (Initial fixation duration bias = 11.72, $SD = 324.32$), $Z = -.55$, $p = .586$. Finally, participants maintained their overall attention equally long on high- and low-calorie food images (274.71 versus 289.55 milliseconds, Gaze dwell time bias = -14.84, $SD = 56.31$), $Z = -1.72$, $p = .086$.

Results do not support an association between the high-calorie spatial memory bias and high-calorie biases in visual attention (**Table A4.5**): A more accurate memory for high-calorie food locations was not predicted by a heightened attention orientation towards high-calorie foods ($B = 69.40$, 95% CI = $[-235.4, 374.2]$), $t(49) = 0.46$, $p = .325$, longer early attention maintenance on high-calorie foods ($B = -0.03$, 95% CI = $[-0.10, 0.03]$), $t(49) = -1.10$, $p = .138$, or prolonged overall attention maintenance on high-calorie foods ($B = 0.06$, 95% CI = $[-0.29, 0.42]$), $t(49) = 0.35$, $p = .364$.

General Discussion

The present research is grounded on the premise that during the course of our evolutionary history as hunter-gatherers, human memory systems evolved mechanisms conducive to energy-efficient foraging. In line with previous observations that support such an adaptive perspective on human memory (Nairne & Pandeirada, 2008; New *et al.*, 2007; de Vries *et al.*, 2020a; de Vries *et al.*, 2020b), our results further substantiate the notion that human spatial memory shows sensitivity to content and prioritizes the locations of high-calorie (and savoury-tasting) nutritional resources. Although individuals were faster at (re)locating high-calorie relative to low-calorie foods in the unfamiliar supermarket, the high-calorie bias in human spatial memory did not directly predict a lower search time for high-calorie foods, or a higher proportion of high-calorie food choice. Rather, a greater expression of the bias was predictive of a lower perceived difficulty of finding high-calorie relative to low-calorie foods in a real-world setting. Furthermore, the magnitude of the high-calorie spatial memory bias did not correlate with a bias in either attention orientation or attention maintenance for high-calorie foods.

The high-calorie bias in human spatial memory was first reported by New *et al.* (2007), who found that the accuracy of recalling food locations improved linearly with the caloric density of a group of “traditionally” gatherable resources (i.e. fruits, vegetables, nuts). The present study replicates the mnemonic effect of caloric content, and demonstrates that it extends to foods more characteristic of the modern environment and of a wider range of energy densities (see also de Vries *et al.*, 2020a and 2020b). Importantly, this suggests that the spatial processing bias is not designed to respond to a fixed repertoire of foods. Rather, it is likely that the mechanism shows sensitivity to the (relative) caloric quality of a food, which we learn to associate with its

other sensory characteristics (i.e. sight or smell) through eating experiences (Myers, 2018; Yeomans, 2006). Indeed, there would be little adaptive value in a foraging mechanism that attaches itself to a fixed array of nutritional resources, as (high-priority) foods do not occur in precisely the same form under varying spatiotemporal circumstances

The savory-taste bias in human spatial memory represents a more recent finding that is speculated to reflect a foraging adaptation for protein-rich resources (de Vries *et al.*, 2020b). Namely, taste modality plays a functional role in the food selection and food intake of many animal species, by signaling the nutritional profile of a specific food: *Sweet* for a sugar- and carbohydrate-rich food, and *savory* for a high amino-acid or protein content (Breslin, 2013; Yarmolinsky *et al.*, 2009). Given that major protein resources in ancestral food environments (e.g. mobile animal prey) had more variable return rates than carbohydrate-rich resources (e.g. immobile fruits), this suggests that it was a bigger adaptive problem for foragers to secure sufficient protein intake to fulfil their relatively high nutritional protein demands (Bird *et al.*, 2009; Cordain *et al.*, 2000; Eaton, 2006; Stiner & Kuhn, 2009). However, as locations of protein-rich foods – including animal prey – can follow a predictable spatial and temporal distribution due to seasonal variations in environmental conditions (e.g. habitual ranging and migration animal patterns; Bracis & Mueller, 2017), we speculate that the savory-taste spatial memory bias could have been adaptive in increasing the chances of successful protein capture (de Vries *et al.*, 2020b).

We expected that if individuals continue to house cognitive adaptations that are mismatched to existing evolutionary novel food-replete conditions, obesogenic consequences on foraging-related behavior could ensue (Eaton *et al.*, 1988; Lieberman, 2006). We found that both objective and perceived search performance were moderately better for (savory-tasting) high-calorie products than low-calorie alternatives that were matched on spatial distributions within the supermarket environment. However, a greater expression of the (lab-tested) high-calorie spatial memory bias was only systematically associated with a lower reported difficulty of finding high-calorie items in the supermarket. The fact that the cognitive bias did not account for the faster localization of high-calorie foods in the field setting may be due to a number of considerations, which are outlined below.

Firstly, whether (smaller-scale) lab-administered tests of spatial ability accurately reflect behavioral indices of navigation in larger real-world settings is unclear. Though moderately strong correlations between psychometric and field-based measures of spatial performance have been reported (Hegarty *et al.*, 2006; Moffat *et al.*, 1998; Murakoshi & Kawai, 2000), spatial information is learned from different visual perspectives (i.e. aerial or map-like perspective in psychometric spatial tasks versus viewer-centered perspective during actual navigation), and distinct spatial memory sub-systems are thought to function at different scales of space (Maguire *et al.*, 1999; Piccardi *et al.*, 2010). Secondly, variation between individuals in their preferred mode of representing spatial information (Bocchi *et al.*, 2019; Pazzaglia & Taylor, 2007), or fluency of using heuristics (e.g. pursuing aisle locations of similar products) to aid incomplete cognitive maps (Conlin, 2009; Murakoshi & Kawai, 2000), could have enabled those with a lower expression of the high-calorie spatial memory bias to compensate for an otherwise higher search time. For instance, goals of the food search task could have been better suited for individuals with a greater affinity for constructing cognitive maps using a certain spatial representation (i.e. landmark, route, or survey “spatial cognitive style”), which would have minimized effects of the high-calorie bias in spatial memory on navigation in those individuals (Pazzaglia & Taylor, 2007). Finally, the larger variation in search times – compared to that of perceived search difficulty ratings (**Table A4.3**) – of our study sample may have compromised the power to reveal a statistically significant effect on the former parameter, and results may likewise have been restricted by using search time as the only proxy for search efficiency. A more robust test could have supplemented time readings with those of a higher specificity for activity-induced energy expenditure (e.g. pedometer; Tudor-Locke *et al.*, 2012), or made use of technology that is able to track real-time indoor movements. As such, it would be fruitful for future investigations to document both quantitative (e.g. spatial orientation ability; Kozlowski & Bryant, 1977) and qualitative (e.g. spatial cognitive style; Pazzaglia *et al.*, 2000) individual differences in navigation-related abilities – as well as include a broader range of performance markers – to finer decompose food searching implications of the spatial processing bias.

In a similar vein, limitations in our operationalization of food choice could have diluted a potential (direct) influence of the high-calorie bias in spatial memory. Despite the covert nature and ecologically valid context of the food choice task, it may have still

elicited strategic choice behavior, owing to the “reward” connotation attached to grocery purchases. That is, although the physical surroundings for selecting foods was appropriate, the situational framing of grocery purchases as an extra gift for participation may have activated “reward” schemas and prompted individuals to deviate away from making habitual food choices (Meiselman, 1996). In light of previous null relationships with single-point measures of food choice (de Vries *et al.*, 2020b), and the significant association of the high-calorie spatial memory bias with a marker of habitual diet quality (i.e. BMI) (Allan & Allan, 2013), it would be worthwhile to probe associations with longer-term eating behavior, as these measures would be less susceptible to instances of opportunistic behavior as well.

Having said that, results reveal a potential novel pathway through which a superior location memory for high-calorie foods could *indirectly* bias future choice preferences towards calorie-rich options. By lowering the perceived difficulty of finding high-calorie items, the high-calorie spatial memory bias could make these options seem relatively more convenient to obtain within a diverse food environment. Convenience, in turn, is an established value that individuals negotiate, and often prioritize, during the food decision-making process (Furst *et al.*, 1996; Sobal *et al.*, 2006). Indeed, our data showed a trend for a negative correlation between the reported difficulty of finding high-calorie items, and the proportion of high-calorie foods individuals later purchased. Thus, the present study yields new mechanistic insights on how the cognitive bias can translate into suboptimal (long-term) dietary outcomes within a modern foraging context (cf. Allan & Allan, 2013). Going forward, it would be interesting to explore possible bias implications on a larger scale of space, by extending investigations beyond a single resource “patch” and towards multiple food locations. For instance, the high-calorie spatial memory bias might also increase the frequency of visits made to unhealthy calorie-laden food locations (e.g. fast-food outlets).

Finally, the high-calorie bias in spatial memory was found to be expressed independently of the amount of attention individuals allocated to high-calorie (versus low-calorie) foods. This finding illustrates another functional design feature of the bias, aside from calorie-sensitivity. Namely, our results align with the operating characteristics of an autonomous or “automatic” spatial mechanism, given that its execution was also not dependent upon “higher level” processes (e.g. consciously articulated dietary preferences or motivations) in the present study (Evans & Stanovich, 2013; New *et al.*,

2007; de Vries *et al.*, 2020a; de Vries *et al.*, 2020b). Collectively, these observations imply that the high-calorie bias in spatial memory may have been adaptive for sustaining a high habitual foraging efficiency, as it does not compete for valuable limited attentional resources that would have been required in other fitness-relevant activities, such as avoiding predators (Evans & Stanovich, 2013; Krasnow *et al.*, 2011). Furthermore, the dissociation of the bias' expression from volitional cognitive processes posits that interventional strategies targeting its downstream translation into eating behaviour may be more effective to pursue for healthy dietary regulation.

Taken together, our findings join an increasing literature base that position a food's energy payoffs as an important factor in the operations of human spatial memory, and make a compelling case for an evolved (food) spatial processing system with calorie-sensitivity and automaticity built-in as functional design features. Such a spatial mechanism that was adaptive in our evolutionary past for energy-efficient foraging may now maladaptively potentiate high-calorie food choice, through altering perceptions of food search convenience.

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Chapter 4

Appendix

Food Pics **Catalogue Numbers**

High-calorie: 2^a, 16^a, 27^a, 44^a, 53^a, 60^a, 104, 116^a, 134^a, 286^a, 400, 517^a

Low-calorie: 199, 233^a, 250^a, 251, 260^a, 274^a, 389^a, 393^a, 407^a, 413^a, 442^a, 453^a

^aUsed in both eye-tracking and spatial memory tasks

Table A4.1.

Eye-tracking Task	Parameter (unit)	High-calorie M (SD)	Low-calorie M (SD)	<i>p</i>
Nutritional Content	Energy density (<i>kcal/100g</i>)	381.5 (109.9)	31.4 (15.6)	<.001
	Total energy displayed (<i>kcal</i>)	763.3 (854.3)	198.6 (339.7)	.016
	Protein to Carbohydrate and Fat Ratio ^a	0.2 (0.3)	0.6 (0.9)	.218
Subjective Ratings	Perceived calories (<i>mm</i>) ^b	76.3 (14.8)	23.8 (16.1)	<.001
	Perceived healthiness (<i>mm</i>) ^b	23.6 (19)	80.4 (15.5)	<.001
	Recognizability (%) ^c	98.4(1.4)	96.8 (5.9)	.902
	Subjective Complexity (<i>mm</i>) ^c	29.6 (6.3)	28.7 (3.7)	.622
Image Characteristics ^b	Color (Red; <i>pixels</i>)	0.5 (0.04)	0.5(0.1)	.539
	Color (Blue; <i>pixels</i>)	0.2 (0.03)	0.2 (0.1)	.740
	Color (Green; <i>pixels</i>)	0.3 (0.1)	0.4 (0.1)	.512
	Size (<i>pixels</i>)	0.3 (0.1)	0.3 (0.1)	.537
	Brightness (<i>luminance</i>)	33.2 (9.1)	36.2 (13.1)	.560
	Contrast (<i>luminance</i>)	49.5 (9.8)	49.3 (13.7)	.960
	Complexity (<i>pixels</i>)	0.1 (0.03)	0.1 (0.04)	.705
	Normalized Complexity (<i>pixels</i>)	0.3 (0.1)	0.3 (0.1)	.650

^a Significantly differed between Sweet (0.11 ± 0.08) and Savory (0.74 ± 0.87) food stimuli ($U = 22$; $p = .035$).

^b Pilot results from a separate participant sample (de Vries *et al.*, 2020b).

^c Data available from the *Food Pics* database (Blechert *et al.*, 2014)

Spatial Memory Task	Parameter (<i>unit</i>)	High-calorie M (SD)	Low-calorie M (SD)	<i>p</i>
Nutritional Content	Energy density (<i>kcal/100g</i>)	382.3 (106.9)	28.5 (15.7)	<.001
	Total energy displayed (<i>kcal</i>)	685.2 (797.5)	181.6 (310.4)	.006
	Protein to Carbohydrate and Fat Ratio ^a	0.2 (0.2)	0.6 (0.8)	.178
Subjective Ratings	Perceived calories (<i>mm</i>) ^b	75.3 (16.1)	23.1 (15.8)	<.001
	Perceived healthiness (<i>mm</i>) ^b	23.5 (18.5)	79.6 (15.4)	<.001
	Recognizability (%) ^c	97.9 (2.1)	96.7 (5.5)	.534
	Subjective Complexity (<i>mm</i>) ^c	29.4 (6.6)	27.7 (4.1)	.331

^a Significantly differed between Sweet (0.11 ± 0.07) and Savory (0.68 ± 0.81) food stimuli ($U = 36$; $p = .039$).

^b Pilot results from a separate participant sample (de Vries *et al.*, 2020b).

^c Data available from the *Food Pics* database (Blechert *et al.*, 2014).

Table A4.2.

High- and low-calorie food products chosen for the supermarket-based food search task.

Caloric Density Condition	Food product (<i>Brand</i>)	Kcal/100 g
High-calorie	Honey (<i>Jumbo Flower Honey</i>)	302 ^a
	Chocolate Cookie (<i>Jumbo</i>)	502 ^a
	Sweet Ice Cream (<i>Ben and Jerry's Cookie Dough S'wich Up</i>)	290 ^a
	Chocolate Wafer (<i>Kit Kat</i>)	515 ^a
	Fried Cheese Pastry (<i>Mora</i> , in Dutch: Kaassoufflé)	301 ^a
	Savory Chicken Cordon Bleu (<i>Jumbo</i>)	251 ^a
	Potato Chips (<i>Pringles Hot & Spicy</i>)	505 ^a
	Salami Slices (<i>Jumbo</i>)	457 ^a
Low-calorie	Sweet Ice Popsicles (<i>Ice Kitchen Peach and Hibiscus Lollies</i>)	55 ^a
	Low-fat Strawberry and Raspberry Quark (<i>Jumbo</i>)	42 ^a
	Oranges	48 ^b
	Pineapple Slices	54 ^b
	Eggplant	20 ^b
	Savory Frozen Garlic Shrimps (<i>Jumbo</i>)	59 ^a
	Frozen Creamed Spinach (<i>Iglo</i>)	54 ^a
	Tomato Cubes (<i>Jumbo</i>)	23 ^a

^a From the Jumbo supermarket website (<https://www.jumbo.com/>)

^b From the Dutch Food Consumption Table (RIVM, 2011)

Table A4.3.

Food search times and perceived search difficulty ratings aggregated by caloric density group.

Caloric Density Condition		Search Time (Seconds)		Perceived Search Difficulty (mm)	
High-calorie	Sweet	Mean	SD	Mean	SD
		48.87	40.21	30.96	24.24
	Savory	46.12	36.62	28.42	22.24
		47.50	38.44	29.69	23.27
Low-calorie	Sweet	Mean	SD	Mean	SD
		49.36	44.72	31.01	26.92
	Savory	59.19	53.95	34.40	27.74
		54.27	49.73	32.70	27.35

Table A4.4.

Predicting high-calorie food choice from the high-calorie bias in spatial memory.

Variable	B	95% CI	Beta	t	p	R	R ²
Model 1:							
Proportion of high-calorie foods purchased and the high-calorie spatial memory bias							
Constant	0.93	.03 – 1.82		2.09	.042 *	.429	.184
Sex ^a	-0.08	-0.26 – 0.09	-0.13	-0.94	.354		
Age	-0.02	-0.05 – 0.01	-0.22	-1.30	.199		
Ethnicity	-0.04	-0.12 – 0.04	-0.15	-0.95	.346		
Hunger	-0.003	-0.01 – 0.002	-0.15	-1.12	.268		
Familiarity High – Low Calorie	0.18	-0.03 – 0.39	0.27	1.74	.089		
Attractiveness High – Low Calorie	0.00	-0.01 – 0.01	-0.01	-0.08	.934		
Eye-Catching High – Low Calorie	0.001	-0.01 – 0.01	0.05	0.32	.752		
Healthy Eating Goals	0.05	-0.04 – 0.15	0.16	1.09	.283		
High-calorie Spatial Memory Bias ^b	-6.75 x 10 ⁻⁵	-0.001 – 0.001	-0.02	-0.12	.905		
Model 2 (exploratory):							
Proportion of high-calorie food costs and the high-calorie spatial memory bias							
Constant	0.87	-0.07 – 1.82		1.85	.070	.408	.167
Sex ^a	-0.09	-0.27 – 0.10	-0.14	-0.98	.333		
Age	-0.02	-0.05 – 0.02	-0.16	-0.96	.342		
Ethnicity	-0.05	-0.13 – 0.04	-0.19	-1.13	.262		
Hunger	-0.003	-0.01 – 0.002	-0.15	-1.11	.271		

Familiarity High – Low Calorie	0.17	-0.05 – 0.39	0.24	1.52	.134
Attractiveness High – Low Calorie	0.001	-0.01 – 0.01	0.06	0.39	.699
Eye-Catching High – Low Calorie	-0.001	-0.01 – 0.01	-0.04	-0.28	.779
Healthy Eating Goals	0.05	-0.05 – 0.15	0.15	1.05	.299
High-calorie Spatial Memory	-8.02 x 10 ⁻⁵	-0.001 – 0.001	-0.02	-0.13	.894
Bias ^b					

Model 3 (exploratory):

Average caloric density of groceries and the high-calorie spatial memory bias

Constant	252.42	-229.69 – 734.53		1.052	.298	.420	.177
Sex ^a	-16.01	-83.96 – 51.93	-0.07	-0.47	.638		
Age	-1.92	-13.19 – 9.36	-0.06	-0.34	.734		
Ethnicity	-19.42	-52.77 – 13.93	-0.21	-1.17	.248		
Hunger	-0.02	-1.81 – 1.77	-0.003	-0.03	.979		
BMI	3.04	-9.99 – 16.06	0.07	0.47	.642		
Familiarity High – Low Calorie	89.37	9.17 – 169.56	0.36	2.24	.030		
					*		
Attractiveness High – Low Calorie	-0.72	-3.48 – 2.05	-0.08	-0.52	.605		
Eye-Catching High – Low Calorie	0.75	-1.67 – 3.17	0.09	0.62	.536		
Healthy Eating Goals	5.02	-31.76 – 41.80	0.04	0.27	.785		
High-calorie Spatial Memory	0.07	-0.37 – 0.52	0.05	0.34	.737		
Bias ^b							

^aMales are the reference group

^b $D_{\text{High Calorie}} - D_{\text{Low Calorie}}$ (Lower values denote a greater bias in spatial memory for high-calorie foods)

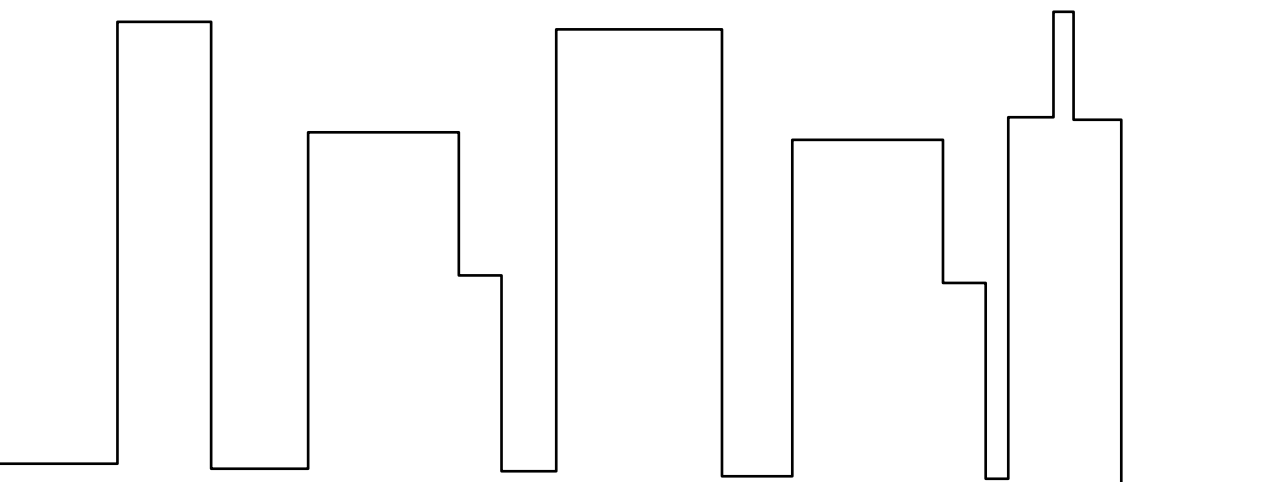
* $p < .05$; ** $p < .01$; *** $p < .001$

Table A4.5.

Predicting the high-calorie bias in spatial memory from high-calorie biases in visual attention.

Variable	B	95% CI	Beta	<i>t</i>	<i>p</i>	R	R²
Constant	-15.86	-268.03 – 236.31		-0.13	.900	.509	.259
Sex ^a	-6.68	-49.05 – 35.69	-0.04	-0.32	.753		
Age	1.48	-4.84 – 7.80	0.07	0.47	.639		
Ethnicity	-10.69	-29.96 – 8.57	-0.18	-1.12	.270		
Spatial Memory Task Order	-42.66	-80.72 – -4.60	-0.32	-2.25	.029*		
Hunger	0.48	-0.43 – 1.39	0.14	1.06	.295		
Desirability High – Low Calorie	-0.43	-1.46 – 0.60	-0.12	-0.83	.408		
Familiarity High – Low Calorie	-6.88	-49.23 – 35.46	-0.05	-0.33	.745		
Gaze direction bias ^b	69.40	-235.39 – 374.18	0.06	0.46	.649		
Initial fixation duration bias ^b	-0.03	-0.10 – 0.03	-0.16	-1.10	.276		
Gaze dwell time bias ^b	0.06	-0.29 – 0.42	0.05	0.35	.727		

^aMales are the reference group^bDifference between high- and low-calorie food images* $p < .05$; ** $p < .01$; *** $p < .001$



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A minimalist line-art graphic at the top of the page. On the left, a series of vertical lines of varying heights form a stylized city skyline. On the right, a location pin icon is shown, with a horizontal line extending from its top towards the right edge of the frame.

Chapter 5

Wired for harsh food
environments: Human spatial
memory favors the effortless
location and consumption of
high-calorie foods

Abstract

Human memory automatically prioritizes locations of high-calorie foods, likely reflecting an adaptation for foraging in harsh ancestral food environments. We investigated whether this high-calorie bias in human spatial memory yields maladaptive consequences for individual eating behavior in present-day food-abundant settings. In an online study, we tested the food spatial memory of a diverse sample of 405 individuals, as well as examined associations between the high-calorie spatial memory bias and the routine frequency of high-calorie snack consumption, exposure to high-calorie food environments, and BMI of a subset of 316 individuals. A greater expression of the high-calorie spatial memory bias predicted a stronger habit of purchasing high-calorie snack foods and consequently a higher individual BMI. Although individuals from various sociodemographic groups expressed the high-calorie bias in spatial memory, our results demonstrate that those with a better inhibitory control to high-calorie foods were protected from bias-induced tendencies to frequent high-calorie food outlets.

Introduction

Our present-day food environment boasts an abundance of cheap, convenient, and highly palatable energy-dense foods – promoting individuals to (over)consume unhealthy high-calorie items (Swinburn *et al.*, 2011). However, not everyone overeats and accumulates excessive body weight, suggesting large differences between individuals exist in the ability to navigate “obesogenic” settings and maintain a healthy energy balance (Swinburn *et al.*, 2011). A novel account for these individual differences proposes that susceptibility to the current food-rich landscape may (partially) stem from a foraging-related adaptation that evolved during our long past as hunter-gatherers. More specifically, from the graded expression of a cognitive adaption that enabled early humans to efficiently locate high-quality resources within harsh ancestral food environments: a prioritization – or “bias” – in spatial memory for high-calorie foods (Allan & Allan, 2013; New *et al.*, 2007b; de Vries *et al.*, 2020a; de Vries *et al.*, 2020b). Here we demonstrate that the “high-calorie bias” in human spatial memory maladaptively influences routine eating behavior within the modern food context, and is expressed by individuals spanning diverse sociodemographic characteristics.

About 99 percent of human evolutionary history is characterized by extensive hunting-gathering activities within a fluctuating food environment, where food availability varied in space and time (Eaton, 2006; Ulijaszek, 2002). In such environments, a fitness advantage was acquired by individuals who evolved (cognitive) mechanisms that maximized the net energy gained during foraging (Schoener, 1971; Winterhalder, 1981). Empirical support for the existence of such an optimized foraging-related cognitive adaptation in humans is growing. Namely, human spatial memory appears to show sensitivity to the energy content of potential foods, and automatically prioritizes the locations of foods higher in caloric quality – irrespective of the sensory nature of food stimuli (i.e. visual versus olfactory food cues), one’s hedonic judgements of a food, past experiences with a food, or deliberate intention (and corresponding time taken) to memorize food locations (New *et al.*, 2007b; de Vries *et al.*, 2020a; de Vries *et al.*, 2020b). It is thought that this high-calorie bias in spatial memory helped hunter-gatherers navigate erratic food habitats, by enabling them to efficiently register and (re)locate valuable calorie-dense resources – without occupying attentional processes needed in other fitness-relevant tasks (e.g. avoiding predators, caring for offspring) (New *et al.*, 2007b; de Vries *et al.*, 2020a; de Vries *et al.*, 2020b).

What was once an adaptive cognitive mechanism for energy-efficient foraging may now operate counterproductively for individuals in urbanized food settings, where high-calorie foods are readily available and accessible (Allan & Allan, 2013; de Vries *et al.*, 2020b; de Vries *et al.*, *under review b*). Allan & Allan (2013) found that a superior memory for high-calorie snack locations (versus that of low-calorie fruits and vegetables) was associated with a higher BMI in women – an objective marker of long-term dietary intake and strong correlate of excess body fat mass (Bouchard, 2007). Furthermore, de Vries *et al.* (*under review b*) showed that individuals (re)located high-calorie products faster than spatially-matched low-calorie products in an unfamiliar supermarket, and a more accurate (lab-tested) memory for high-calorie versus low-calorie food locations was associated with a greater ease of finding high-calorie products in the supermarket. On the other hand, null associations between the high-calorie spatial memory bias and (primarily) lab-based and single time point measures of eating behavior have also been observed (de Vries *et al.*, 2020b; de Vries *et al.*, *under review b*). However, the latter may have resulted from the constrained spatiotemporal circumstances in which food decisions were investigated. Thus, to offset incidental responses and gain insight into an individual's routine eating behavior, this study probed associations with longer-term eating-related parameters (i.e. frequency of high-calorie snack consumption in the past month, exposure to high-calorie food environments in the past month, and BMI) that covered a range of typical physical and situational food decision-making contexts.

If the high-calorie bias in human spatial memory is indeed linked to undesirable behavioral and health outcomes at present, it would be of relevance to identify “at-risk” subpopulations that demonstrate a great expression of the cognitive bias. Studies to date have mainly utilized smaller samples of young, majority-female, highly-educated, and health-minded individuals (cf. Allan & Allan, 2013; de Vries *et al.*, 2020b; de Vries *et al.*, *under review b*), which questions whether an equivalent expression of the high-calorie spatial memory bias can be extrapolated to other sociodemographic groups that are exposed to systematically different structural (e.g. built food environments) and social (e.g. food norms) conditions. That is, the evolutionary account of the spatial processing bias suggests its general presence across individuals, but the graded expression of the bias may be a function of the food environment one is exposed to, which is well-documented to follow a sociodemographic gradient. For instance, the

local food environments of individuals who live or school in low socioeconomic status (SES) neighborhoods consist of a higher density of fast-food outlets, as well as a greater number of promotions and public advertisements featuring unhealthy energy-dense foods (Larson *et al.*, 2009; Timmermans *et al.*, 2018; Yancey *et al.*, 2009). In addition, individuals with a lower income, education, occupation, perceived social status, or who live in disadvantaged areas display suboptimal diets and higher (less healthy) BMI (Adler *et al.*, 2000; Drewnowski *et al.*, 2014; Janssen *et al.*, 2006; Lakerveld *et al.*, 2015). A novel contributing factor to the discrepancy in dietary quality between sociodemographic groups could be a difference in the degree to which the high-calorie spatial memory bias is expressed (and interacts with varying aspects of one's local food environment) to influence routine eating behavior.

That being said, earlier observations also indicate that the translation of the high-calorie spatial memory bias into eating behavior is not always straightforward, and a more nuanced account of behavioral pathways involving psychological process moderators may be warranted (de Vries *et al.*, 2020b). "Controlled" consciously-deliberated psychological factors, such as an individual's explicit intentions to eat healthy, could play a role in countering (or antagonizing) obesogenic tendencies induced by the cognitive bias (de Vries *et al.*, 2020b). Moreover, the high-calorie spatial memory bias might potentiate high-calorie food choice by making these options seem more convenient to obtain in a diverse food environment (de Vries *et al.*, *under review b*). Thus, a boundary condition for the bias to take effect could be a sufficiently high (deliberated) importance of "convenience" to the food decision making of individuals (Furst *et al.*, 1996). By the same token, automated psychological processes, which require limited conscious deliberation or minimal cognitive resources, may stimulate or inhibit behavioral outcomes. A stronger pre-existing habit of choosing (or purchasing) high-calorie snack foods might synergize adverse bias implications, by increasing the likelihood of these behavioral responses in certain contexts (Verplanken & Orbell, 2003). Conversely, an individual's ability to successfully inhibit impulsive responding to high-calorie foods – such as those supposedly elicited by the high-calorie spatial memory bias – could protect against its negative effects (Batterink *et al.*, 2010). However, these interactions have yet to be formally tested.

In short, the present research had three objectives. Our first objective was to investigate the effect of the high-calorie spatial memory bias on individuals' routine

eating behavior (i.e. high-calorie snack consumption frequency, exposure to high-calorie food environments, and BMI). Secondly, we examined the expression of the high-calorie bias in human spatial memory in a diverse sample of (Dutch) individuals with varying sociodemographic characteristics. Finally, we considered whether specific psychological factors moderate behavioral effects of the high-calorie spatial memory bias. We hypothesized that:

H_1 : The high-calorie spatial memory bias predicts a greater routine frequency of high-calorie snack consumption, greater routine exposure to high-calorie food environments, and a higher BMI in individuals.

H_2 : The magnitude of the high-calorie bias in human spatial memory varies across sociodemographic characteristics.

H_3 : Psychological factors moderate effects of the high-calorie spatial memory bias on routine eating behavior. A higher importance of convenience in food choice, as well as greater snack purchasing habit strength, will synergize behavioral effects of the high-calorie spatial memory bias. Conversely, a higher healthy eating intention and greater inhibitory control to high-calorie foods will antagonize behavioral effects of the high-calorie spatial memory bias.

Methodology

Design

The present study had a repeated measures design with *Caloric Density* (High versus Low) as a within-subjects factor. In an online experiment, participants had to complete a sequence of cognitive tasks and questionnaires in two test sessions, with a washout period of approximately one week. The hypotheses, experimental design, and statistical analysis plan were preregistered, and are available with data that support the findings of this study on the Open Science Framework database (Project URL: <https://osf.io/nv7a9/>).

Participants

Participants were a diverse sample of healthy Dutch adults (above the age of 18) living in the Netherlands, recruited via stratified sampling (i.e. on sex, age, education level, and province) by the ISO-certified *Flycatcher* online research agency (www.flycatcher.eu). Individuals were not allowed to participate if they self-reported any dietary restrictions, a current or medical history of eating disorders, or (total or partial) color blindness. A total of 613 individuals were initially invited, and a response rate of

66.1% was achieved. Thus, 405 individuals (56.7% Male; $M_{\text{Age}} = 47.57 (\pm 17.48)$ years, Range: 18 – 86 years; $M_{\text{BMI}} = 25.96 (\pm 4.71)$ kg/m²; Range: 18.12 – 59.52 kg/m²) took part in the first session that tested food spatial memory. Of the initial sample, 321 individuals returned for the second test session (corresponding to a drop-out rate of 20.7%), but five participants were excluded due to incomplete data. As a result, data from 316 participants (57.9% Male; $M_{\text{Age}} = 47.37 (\pm 17.64)$ years, Range 18 – 86 years; $M_{\text{BMI}} = 25.86 (\pm 4.59)$ kg/m²; Range: 18.12 – 47.32 kg/m²) were used for analyzing behavioral outcomes. *A priori* power calculations (see <https://osf.io/byuhe> for details) required a minimum sample size of 312 individuals, and final participant samples (between test sessions) were well-matched on sociodemographic distributions (**Table A5.1**). After providing informed consent and completing the online experiment, participants were financially compensated. This study was approved by the Social Sciences Ethics Committee of Wageningen University.

Procedure

A general research aim was advertised to participants before testing, stating that the study was interested in "*what people think about the modern food environment and the foods typically found within it*". In the first online test session, participants filled out a preliminary questionnaire asking background characteristics (e.g. height, weight, subjective SES). Next, they provided ratings on hunger state, as well as on (randomly-presented) food stimuli (N=24) on the aspects of *Liking*, *Desire to Eat*, and *Familiarity*. Finally, individuals performed the spatial memory task for both high- and low-calorie foods, with a five-minute rest between conditions. The first session took approximately 40 minutes.

In the second test session, approximately one week later, participants first recorded their hunger state. Individuals then had to complete the food-specific go/no-go task and five questionnaires (i.e. snack FFQ, food environment visits, importance of convenience, snack purchasing habit strength, and healthy eating intentions) in a randomized manner, to circumvent possible order effects on answering. The second session took approximately 20 minutes.

Apparatus and Stimuli

Food stimuli in cognitive tasks. Standardized images depicting high- and low- calorie foods were sourced from the *Food Pics* database¹ (Blechert *et al.*, 2014). Consistent with earlier investigations (de Vries *et al.*, 2020a; de Vries *et al.*, 2020b; de Vries *et al.*, *under review b*), items were considered high-calorie if they contained at least 225 kcal – and low-calorie if they contained at most 60 kcal – per 100 grams of food.

For cognitive tasks, a set of 24 (unbranded) food pictures was used as food stimuli, with 12 images for each caloric density category (de Vries *et al.*, *under review b*). Importantly, an equal number of sweet and savory items were present across caloric density groups (e.g. *High-calorie*: hamburger and chocolate bar; *Low-calorie*: tomato and watermelon), as (spatial) memory mechanisms may respond to taste modalities differently (Meule *et al.*, 2012a; de Vries *et al.*, 2020b; de Vries *et al.*, *under review b*). High- and low-calorie food stimuli were equivalent in macronutrient balance (i.e. protein to carbohydrate and fat ratios; Simpson & Raubenheimer, 2005), recognizability, and a wide range of image characteristics (see **Table A5.2** in the Supplemental Material). Conversely, high-calorie food images displayed a greater energy density (kcal/100g) as well as total energy content (kcal), and were correctly perceived to contain more calories and to be less healthy compared to low-calorie alternatives in a separate pilot study (**Table A5.2**).

Spatial memory task. The computer-based spatial memory task has been validated for use in the target population in previous studies (Allan & Allan, 2013; de Vries *et al.*, 2020b; de Vries *et al.*, *under review b*). For the task, participants were instructed to imagine that an international food market with 24 food stalls was taking place within an (unfamiliar) university campus setting. They were then shown 12 images of either high-calorie or low-calorie foods, followed by an image of the university campus map showcasing all 24 possible stall locations, at a fixed duration of three seconds each.

¹*Food Pics* Catalogue Numbers

High-calorie: 2, 16, 27, 44, 53, 60, 104, 116, 134, 286, 400, 517

Low-calorie: 199, 233, 250, 251, 260, 274, 389, 393, 407, 413, 442, 453

Non-food: 1086, 1094, 1129, 1143, 1155, 1210

Next, the location of the stall selling a food item was indicated on the campus map by a green crosshair, and this was done in a sequential manner for all food stimuli within a caloric density condition (N=12). After a two-minute rest, participants performed a series of 12 spatial memory tests, in which they were randomly-presented with one of the previous food images and required to click on its correct assigned stall location on the campus map. All possible stall sites were displayed anew each recall round, and participants could select the same stall location more than once, even though locations did not overlap between foods. Following a five-minute intermission, participants repeated the spatial encoding and recall procedure for the remaining 12 foods of the other caloric density condition. Task stimuli (i.e. food-locations pairs within the campus map), as well as the stimuli presentation order, were randomized differently for each participant. The order in which participants completed the spatial memory task between caloric density categories was also counterbalanced. Prior to the actual task, participants first practiced encoding and recalling locations of non-food objects on the campus map, to familiarize themselves with the spatial memory paradigm.

Food-specific go/no-go task. The food-specific go/no-go task used to measure inhibitory responses to high-calorie foods was adapted from Chen *et al.*, 2018. The task consisted of one practice block and six experimental blocks in total.

First, participants underwent a practice block consisting of six (randomized) trials with non-food images¹, in order to associate “go” responses (i.e. spacebar press) and “no-go” responses (i.e. no spacebar press) with specific cues (i.e. a blue or grey-colored image border). The assignment of a (blue or grey) border color as a “go” or “no-go” cue was counterbalanced across participants. At the onset of a trial, an image appeared immediately on the screen and a (blue or grey) colored border was presented after 150 milliseconds. Both image and border were then shown for 1500 milliseconds, followed by a fixation cross. To facilitate accurate performance on the task (Wodka *et al.*, 2009), we jittered the duration of the fixation cross between trials (i.e. from 1000 to 1500 milliseconds, in 100 millisecond increments). A minimum number of practice trials ($\geq 80\%$) needed to be successfully responded to before individuals could proceed on to the experimental phase, and feedback was provided during practice trials.

During experimental blocks, low-calorie food images (N=12) were consistently paired with a “go” cue, and high-calorie food images (N=12) with a “no-go” cue. Participants were instructed to respond as quickly and accurately as possible to the cues

after the presentation of a food image. Each experimental block encompassed 24 trials, with each food image appearing once in a randomized order, resulting in 144 experimental trials (N=72 for both high- and low-calorie stimuli) per participant. Unlike the practice block, feedback was not given during experimental trials.

Measurements

Primary outcome variables. Routine frequency of high-calorie snack consumption was gauged using a modified snack-specific food frequency questionnaire, that was designed and validated for use in the Dutch population (Dutch snack FFQ; Streppel *et al.*, 2013). Individuals had to specify how frequently in the past month they consumed a wide range of (sweet and savory) high-calorie snack foods commonly eaten in the Netherlands (e.g. baked goods, chocolate bars, cheese, and potato chips). Response categories spanned from “none” to “six to seven times per week”. The frequency of consumption was averaged across all snack foods for each participant.

A food environment questionnaire was developed to assess routine exposure to high-calorie food environments. The questionnaire asked individuals to indicate the frequency of visits made within the past month to a range of (randomly-presented) physical food retail outlet types typically found in the Netherlands (e.g. supermarket, cafeteria; see *Food Environment Questionnaire* in the Supplemental Material (**Appendix Chapter 5**); USDA Foreign Agricultural Service, 2017). The questionnaire was piloted in a separate sample of Dutch individuals (N = 35; 51.4% Male; M_{Age} = 22.03 (\pm 2.79) years) to ensure that selected food retail outlet types were sufficiently recognizable. The classification of a food retail outlet as a “high-calorie food environment” was advised by guidelines on healthy food environments from the Netherlands Nutrition Centre Foundation (*Voedingscentrum*), and was centered on the availability criterion (Voedingscentrum, 2020). Namely, we classified high-calorie food environments as those having more than 40% of “unhealthy” high-calorie products on offer, the latter defined as (high-calorie) foods that are not included in the *Wheel of Five* Dutch dietary guidelines (Brink *et al.*, 2019; Voedingscentrum, 2020). As such, a more conservative approach was adopted during classification, such that we only considered outlets that offer an overrepresentation of energy-dense foods (e.g. fast food outlets and confectionary stores; N=13 in total) as high-calorie food environments. Our final classification was cross-checked – and confirmed to be in line with – expert-

derived “healthiness scores” of urban Dutch food outlet types (Timmermans *et al.*, 2018). As with the snack FFQ, response categories spanned from “none” to “six to seven times per week”, and the frequency of visits to high-calorie food locations in the past month was averaged per individual.

In addition, individuals self-reported their height (cm) and weight (kg), in order to obtain information on BMI (kg/m²).

Predictor variables. Spatial memory accuracy for high- and low-calorie foods was determined by averaging the ‘pointing error’ or Euclidian distance (D) between correct and recalled stall locations of each food group (Allan & Allan, 2013; de Vries *et al.*, 2020b; de Vries *et al.*, *under review b*). Therefore, *lower* D scores correspond to a *higher* accuracy in food spatial memory. The high-calorie bias in spatial memory was calculated by taking the difference in spatial memory accuracy for high- and low-calorie foods ($D_{\text{High Calorie}} - D_{\text{Low Calorie}}$). As such, *lower* (negative) values denote an *enhanced* memory for high-calorie food locations.

We adapted the food choice questionnaire (Stephoe *et al.*, 1995) to measure the importance of convenience to the food decision making process of individuals. Participants had to rate five statements, such as “It is important to me that the food I eat on a typical day is easily available in shops and supermarkets”, on a four-point scale (from “Not Important At All” to “Very Important”). Responses were averaged, with larger values representing a higher importance attached to convenience in food choice. The questionnaire showed a good internal consistency in our sample (Cronbach’s $\alpha = 0.84$).

Snack purchasing habit strength was assessed with an adapted version of the self-reported habit index (SRHI), which focused on the core SRHI elements of frequency and automaticity (Verplanken & Orbell, 2003; de Vet *et al.*, 2015). “Snacks” were explicitly defined as high-calorie items through the provision of examples (e.g. chips, cookies, candy, and fries) on questionnaire instructions. The questionnaire inquired about (high-calorie) snack purchasing behavior, and comprised of six items that individuals had to rate on a five-point scale (ranging from “Strongly Disagree” to “Strongly Agree”). Sample statements include “Buying snacks is something I do frequently” and “Buying snacks is something I do without thinking”. Separate scores on scale items were averaged, with a higher overall score indicating a greater snack purchasing habit strength. The questionnaire displayed a good internal consistency (Cronbach’s $\alpha = 0.92$).

Participants' healthy eating intentions were recorded with two items (i.e. "In my daily life, I strive to eat healthy" and "It is important to me to eat healthy foods") rated on a seven-point scale anchored from "Strongly Disagree" to "Strongly Agree" (Raghoobar *et al.*, *under review*).

An individual's inhibitory control to high-calorie foods was established by calculating the rate of commission errors (i.e. number of failures of inhibition divided by the total number of no-go trials) committed in the food-specific go/no-go task (Batterink *et al.*, 2010; Chen *et al.*, 2018). A *higher* proportion indicates a *lower* ability to inhibit responses towards high-calorie food stimuli.

Finally, we collected sociodemographic information on sex, age, ethnicity, objective SES (i.e. annual household income, highest education level, and occupation), subjective SES (10-point MacArthur Subjective Social Status Scale; Adler *et al.*, 2000), and neighborhood SES (**Table A5.1**). Household income was composed of five categories: (1) minimum (less than 14,100 euros per year), (2) below the national average (14,100 – 36,500 euros per year), (3) approximately the national average (36,500 – 43,500 euros per year), (4) one to two times the national average (43,500 – 73,000 euros per year), and (5) two or more times the national average ($\geq 73,000$ euros per year). Highest education level followed the Dutch education classification system and was coded as 11 categories, spanning from (1) none or primary school education to (11) university master, doctoral, or postdoctoral (**Table A5.1**). Occupation was categorized into two groups: (1) employed and (2) unemployed. Due to the absence of income information on 71 participants (22.5%) of the second test session, and the lower robustness of linear regression models to missing data (Hughes *et al.*, 2019), objective SES was operationalized as a composite measure (i.e. by standardizing each available variable and taking their mean; Adler *et al.*, 2000) in the analysis of behavioral outcomes. Neighborhood SES was obtained from individual postal codes, which were translated into respective (z-distributed) neighborhood SES scores using the *Statusscores* database of the Netherlands Institute for Social Research (SCP Statusscores, 2017).

Control measures. As hedonic valuations of – and previous experiences with – a food can impinge on the accuracy of recalling its location (de Vries *et al.*, 2020a; de Vries *et al.*, 2020b), we required participants to rate each food stimulus along the parameters of Liking and Desire to Eat on a 100mm VAS (anchored from "Not At All" to "Very Much"), as well as Familiarity on a five-point scale (Tuorila *et al.*, 2001).

Furthermore, hunger states at the onset of testing were documented using a 100mm VAS (anchored from "Not At All" to "Very Much").

Data Analysis

Data analysis was conducted with IBM SPSS Statistics 25. Statistical significance was defined as $p < .05$, with the exception of the second and third confirmatory analyses, which made use of a Bonferroni correction for multiple ($N=3$) behavioral outcomes. The α_{adjusted} for the latter two tests was therefore set at .017. We first examined the existence and expression of the high-calorie spatial memory bias in our sample, before dissecting the bias' behavioral implications.

Expression of the High-calorie Spatial Memory Bias. To demonstrate the existence of a high-calorie bias in human spatial memory, we analyzed food spatial memory data using a linear mixed effects model (LMM), due to its flexibility and robustness in modelling continuous correlated outcomes (Krueger & Tian, 2004). Our saturated LMM comprised of a random intercept and slope with main and interaction effects of *Caloric Density* and *Taste* as fixed factors, *Participant* and *Time* as random factors (covariance structure: Unstructured), *Sex*, *Age*, *Ethnicity*, *Household Income*, *Education*, *Occupation*, *Subjective SES*, *Neighborhood SES*, *Liking*, *Desirability*, *Familiarity*, and *Hunger* as covariates, and $\log_{10}(y+1)$ transformed *Spatial Memory Accuracy (D)* as the dependent variable. To test for sociodemographic moderators of the bias, we entered respective interactions between *Caloric Density* and all sociodemographic factors as additional fixed effects.

The model selection process made use of a backward stepwise approach. First, the covariance matrix of random effects in the saturated LMM was determined using Restricted Maximum Likelihood (REML) ratio tests using the -2 log likelihood (-2LL) test statistic. Then, the fixed part of the saturated LMM was simplified based on Maximum Likelihood (ML) ratio tests using the -2LL test statistic. In both cases, the most parsimonious model was selected and the final LMM was refitted with REML estimations. The finalized LMM was cross-checked with a forward stepwise modelling method.

High-calorie Spatial Memory Bias and Routine Eating Behavior. To test whether the high-calorie bias in spatial memory predicts routine eating behavior, we carried out a multiple linear regression analysis on each outcome variable ($N=3$), with *Sex*, *Age*, *Ethnicity*, *Objective SES* (composite), *Subjective SES*, *Neighborhood SES*, *Liking of high- vs low-calorie foods*, *Desirability of high- vs low-calorie foods*, *Familiarity*

with high- vs low-calorie foods, Importance of Convenience, Snack purchasing habit strength, Healthy Eating Intentions, Inhibitory Control, and the High-calorie spatial memory bias ($D_{\text{High Calorie}} - D_{\text{Low Calorie}}$) as predictor variables.

As models for high-calorie food environment exposure and BMI violated the assumption of homoskedasticity, we performed regression analyses using the “HC 3” heteroskedasticity-consistent standard error estimator (Hayes & Cai, 2007).

High-calorie Spatial Memory Bias, Psychological Moderators, and Long-term Eating Behavior. To determine whether individual psychological factors moderate potential effects of the high-calorie spatial memory bias on routine eating behavior, we included respective interactions between the *High-calorie spatial memory bias* ($D_{\text{High Calorie}} - D_{\text{Low Calorie}}$) and *Importance of Convenience*, *Snack purchasing habit strength*, *Healthy Eating Intentions*, and *Inhibitory Control* as additional predictors in previous multiple linear regression models.

Again, regression analyses for high-calorie food environment exposure and BMI employed robust (HC3-generated) standard errors.

Results

The high-calorie bias in human spatial memory is replicated and equally expressed across sociodemographic groups.

The average accuracy in spatial memory (i.e. pointing error or D) observed across food stimuli was 236.35 ($SD = 217.44$; Range = 0 – 1370.43) pixels.

The caloric density of a food positively predicted how accurate its location was recalled, as individuals demonstrated 4.67% lower pointing errors on average for high-calorie food locations compared to low-calorie counterparts, $F(1,308) = 5.66$, $p = .018$, $\eta^2 = 0.02$, 90%CI $\eta^2 = [0.002, 0.05]$. The high-calorie bias in spatial memory, though small in size, remained significant after controlling for demographic characteristics, hunger state, hedonic food evaluations, and familiarity with foods. In contrast, spatial memory accuracy was not affected by the Taste (i.e. sweet or savory) of a food item, $F(1,6796) = 2.51$, $p = .113$. Among the tested covariates, only Education, $F(1,306) = 16.99$, $p < .001$, $\eta^2 = 0.05$, 90% CI $\eta^2 [0.02, 0.10]$, and Age, $F(1,306) = 31.53$, $p < .001$, $\eta^2 = 0.09$, 90% CI $\eta^2 [0.05, 0.15]$, influenced overall food spatial memory to a similar degree as Caloric Density. A higher education level corresponded to having 3.50%

lower pointing errors on average, whereas a unit increase in age yielded a 0.81% rise in pointing errors.

None of the interactions between Caloric Density and sociodemographic factors (e.g. Sex, Age, Education) reached significance, indicating that the magnitude of the high-calorie spatial memory bias did not differ across sociodemographic groups (all $p > .05$).

The high-calorie bias in human spatial memory does not directly predict routine snack consumption frequency, high-calorie food environment visits, or BMI.

Participants consumed high-calorie snack foods an average of 3.50 ($SD = 1.94$; Range = 0.16 – 10.03) times in a month, and visited high-calorie food environments to eat or purchase foods an average of 0.5 ($SD = 0.65$; Range = 0 – 7.15) times in a month.

No evidence was found for a direct (main) effect of the high-calorie spatial memory bias on the frequency of high-calorie snack consumption in a month, $B = 0.001$, 95% CI = [0.001,0.003], $t(301) = 0.92$, $p = .181$ (**Table A5.3**). Furthermore, an enhanced memory for high-calorie food locations did not directly result in more frequent exposure to high-calorie food environments, $B = 0.00$, 95% CI = [0.00, 0.001], $t(301) = 1.14$, $p = .128$ (**Table A5.4**), or a higher BMI in individuals, $B = -7.29 \times 10^{-5}$, 95% CI = [-0.01, 0.01], $t(301) = -0.03$, $p = .489$ (**Table A5.5**).

Inhibitory control moderates the effect of the high-calorie spatial memory bias on routine high-calorie food environment visits.

Participants reported a medium snack purchasing habit strength of 2.17 ($SD = 0.89$; Range = 1 - 5), an above-average importance of convenience when making food decisions ($M = 2.71 (\pm 0.59)$, Range: 1.2 – 4.0), and a high intention to eat a healthy diet in daily life ($M = 5.31 (\pm 1.07)$, Range: 1 – 7). Finally, the mean commission error rate observed in the food-specific go/no-go task was 0.02 ($SD = 0.05$; Range = 0 – 0.58), amounting to a mean of 1.44 failed no-go trials ($SD = 3.6$; Range = 0 – 42).

Taking psychological constructs into account as possible moderators of behavioral effects, we observed a significant interaction between the high-calorie spatial memory bias and inhibitory control, $B = -0.02$, 95%CI = [-0.03, -0.003], $t(297) = -2.38$, $p = .009$, as well as a trend for a moderating role of snack purchasing habit strength, $B = 0.001$, 95%CI = [1.98×10^{-5} , 0.002], $t(297) = 2.02$, $p = .023$, on the frequency of visits

to high-calorie food environments in a month. Interaction terms between the high-calorie spatial memory bias and all possible moderators, in either high-calorie snack consumption frequency or BMI models, were otherwise not significant (all $p > .017$; **Tables A5.3** and **A5.5**).

Follow-up simple slopes analysis on the significant interaction revealed that individuals with low commission error rates (i.e. high inhibitory control towards high-calorie foods) visit high-calorie food environments *less regularly* as expression of the high-calorie spatial memory bias *increases*, $B = 0.001$, $p = .001$. Furthermore, exploratory (simple slopes) analysis into the trending moderation by snack purchasing habit strength showed opposing effects to the high-calorie spatial memory bias: individuals with a greater habit strength visit high-calorie food environments *less regularly* as expression of the high-calorie bias in spatial memory *increases* (and visit high-calorie food environments *more regularly* as expression of the high-calorie spatial memory bias *decreases*), $B = 0.001$, $p = .017$.

The high-calorie spatial memory bias indirectly predicts a higher BMI, by promoting a greater snack purchasing habit strength.

Guided by the counterintuitive observation that snack purchasing habits seemingly minimize effects of the high-calorie spatial memory bias on high-calorie food environment visits, we further explored the relationship between the two predictors.

A Spearman's correlation revealed, albeit weakly, that as expression of the high-calorie bias in spatial memory increases, so does snack purchasing habit strength, $r_s(316) = -0.11$, $p = .049$ (**Table A5.6**). As snack purchasing habit strength was shown to predict BMI in prior confirmatory analysis (**Table A5.5**), we reasoned that it could act as an intermediary component within the behavioral pathway. Therefore, we tested for an *indirect* association between the high-calorie spatial memory bias and BMI, via an individual's snack purchasing habit strength. Mediation analysis was carried out using the bias corrected bootstrapping method – producing 95% bias corrected confidence intervals for the total indirect association, derived from 5,000 bootstrap resamples (Hayes, 2017). Results yielded a significant indirect effect of the high-calorie spatial memory bias on BMI that was mediated by snack purchasing habit strength, $B = -0.001$, 95% CI $[-0.003, -0.0002]$. An enhanced memory (i.e. lower pointing errors) for high-calorie food locations predicted a greater snack purchasing habit strength ($B = -0.001$, $p = .037$), and consequently a higher individual BMI ($B = 1.07$, $p < .001$).

Discussion

We demonstrate once again that human memory inherently gives priority to locations of foods with high energy-payoffs. (New *et al.*, 2007b; de Vries *et al.*, 2020a; de Vries *et al.*, 2020b; de Vries *et al.*, *under review b*). More importantly, our findings attest to the maladaptive quality of this high-calorie bias in human spatial memory within a modern foraging context, as a greater expression of the bias predicted a stronger habit of purchasing high-calorie snack foods and a higher subsequent BMI (H_1). The expression of the high-calorie spatial memory bias was similar across sociodemographic characteristics (H_2), and we found variation in the circumstances under which the bias translates into routine eating behavior (H_3). Specifically, individuals with a high ability to inhibit impulsive responses to high-calorie foods were shielded from bias-induced tendencies to frequent high-calorie food outlets (**Figure 5.1**).

We provide the first mechanistic insights into how an (inbuilt) superior memory for high-calorie food locations impacts present-day eating behavior in obesogenic food environments. Contrary to expectations, the main effect of the high-calorie spatial memory bias on BMI was *indirect* in nature, and snack purchasing habit strength played a mediating (as opposed to moderating) role in this regard. A defining feature in the development and strengthening of a habit is when a behavioral response is sufficiently and satisfactorily repeated within a specific context, until the point of “automaticity” in which solely environmental cues can elicit the corresponding behavior (Verplanken & Arts, 1999; Verplanken & Orbell, 2003). Therefore, our results collectively suggest that it is not merely the frequency of high-calorie food choice that is targeted. Rather, it is a high frequency *coupled* with a high automaticity of choosing to consume high-calorie foods within a specific context, that forms an essential component in behavioral pathways of the bias. In other words, adverse implications of the high-calorie spatial memory bias likely stem from its ability to automatize certain patterns of undesirable responses in particular situations; the bias may strengthen the mental association between a specific environmental cue (i.e. sight or smell of a high-calorie snack food) and unhealthy behavior (i.e. purchasing the snack food), when a “goal” such as satisfying (physiological or hedonic) hunger is activated.

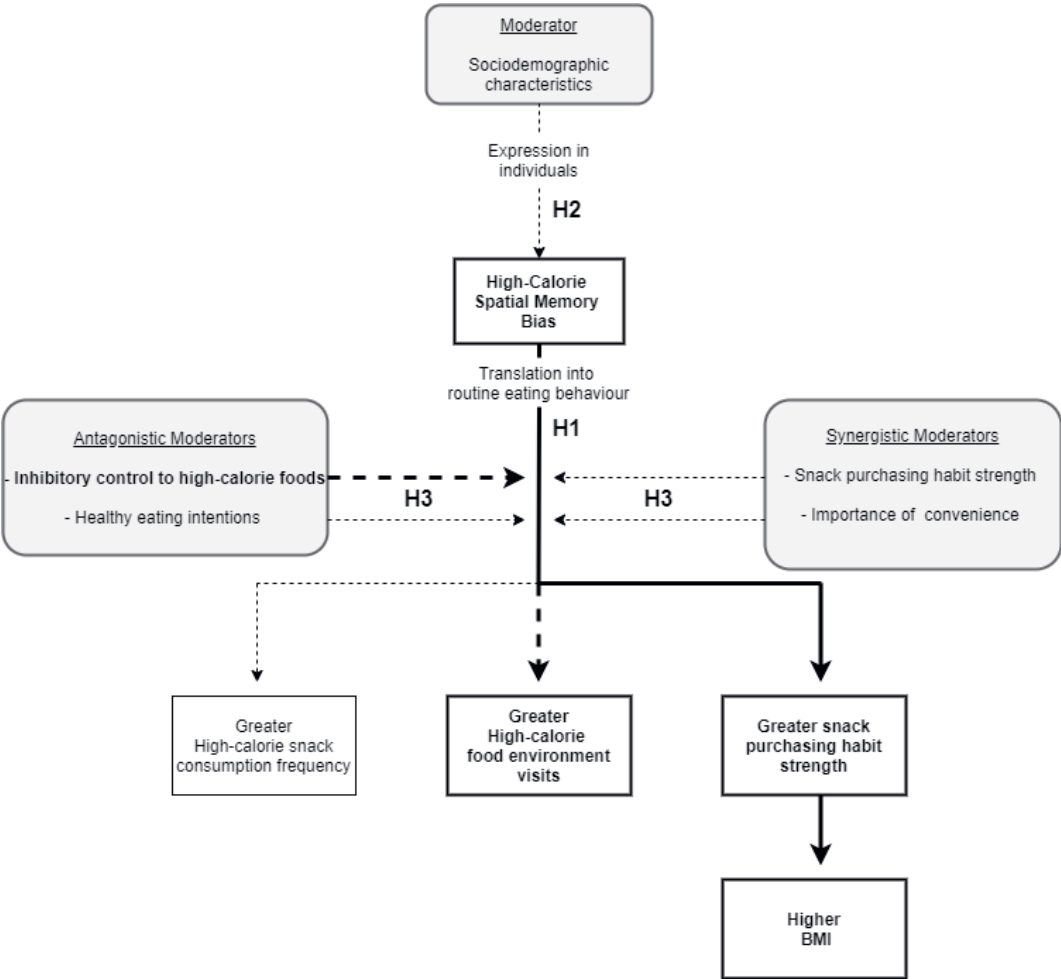


Figure 5.1. Synthesis of main findings. Relationships shown by bolded lines were significant. The high-calorie bias in human spatial memory was replicated and expressed to a similar degree across sociodemographic groups. In turn, the high-calorie spatial memory bias indirectly predicted a higher BMI, by fostering a stronger habit of purchasing high-calorie snack foods (*bolded unbroken line*). Furthermore, the cognitive bias (directly) predicted greater routine visits to high-calorie food outlets, but this effect was antagonized by an individual’s inhibitory control to high-calorie foods (*bolded broken line*).

Consequently, the cognitive bias and its immediate downstream psychological targets are expected to fall under the category of automated “impulsive” drivers of dietary behavior (Evans & Stanovich, 2013; Hofmann *et al.*, 2009; Strack & Deutsch, 2004). In the psychology literature, a distinction is made between estimates of the variance in health-related behavior that can be attributed to automated versus controlled “reflective” processes (Armitage & Conner, 2001; Hardeman *et al.*, 2002;

Sheeran *et al.*, 2001). Although estimates vary, it is generally agreed upon that both classes of processes compete with one another to gain control over resulting behavior when in conflict (Evans & Stanovich, 2013; Hofmann *et al.*, 2009; Nederkoorn *et al.*, 2010; Strack & Deutsch, 2004). The discovery that the implicit high-calorie spatial memory bias propels us to visit energy-rich food environments by default, unless intervened upon by an individual's controlled effort to inhibit impulsive responses to high-calorie foods, complements such a dual-systems perspective. Relatedly, although behavioral changes produced by the spatial processing bias appear small, these outcomes are specific for a one-unit (pixel) increase, which is not representative of the actual scale of bias differences between individuals. Individuals deviated in their expression of the high-calorie spatial memory bias at a magnitude of 102 pixels on average, resembling estimates from previous investigations (de Vries *et al.*, 2020b; de Vries *et al.*, *under review b*). Accordingly, a bigger impact on eating-related parameters is forecasted in practice, and possibly even further exacerbated in situations where "reflective" goal-oriented psychological systems are typically impaired (e.g. during energy-depleted states; Hoffman *et al.*, 2009).

The fact that the high-calorie spatial memory bias was reproduced in a large sample of individuals with diverging sociodemographic characteristics adds substantial internal and external validity to previous demonstrations of the bias. Indeed, the effect of caloric density on food spatial memory accuracy was comparable in size to that of earlier studies with smaller and more homogeneous participant samples (de Vries *et al.*, 2020b; de Vries *et al.*, *under review b*). The mnemonic value of a food's caloric quality was likewise not explicated by effects of general learning mechanisms, such as the motivational salience or familiarity of a food, which can similarly aid spatial memory performance (Craik & Lockhart, 1972; de Vries *et al.*, 2020a; de Vries *et al.*, 2020b; de Vries *et al.*, *under review b*). Thus, our findings also lend credibility to functional (or adaptive) considerations of human memory (Nairne, 2010; Nairne & Pandeirada, 2008b). Still, to strengthen an adaptive evolutionary account of the high-calorie spatial memory bias further, future research could compare its expression in cultures that differ widely on spatial cognitive strategies, as well as perceptions and attitudes towards food. The observation of congruent findings in spite of culture-specific differences would empirically bolster the idea that the spatial processing bias represents a (universally expressed) cognitive adaptation (Nairne, 2010).

More pragmatically, because our results show that the mnemonic effect of caloric content was equivalent across sociodemographic groups, this implies that variation at the level of (overall) bias expression most likely originates from added influences of general learning processes (e.g. food liking, wanting, and familiarity) on food spatial memory. Besides caloric density, hedonic evaluations and past exposures to a food also respectively determine the overall accuracy of recalling its location in space (de Vries *et al.*, 2020a; de Vries *et al.*, 2020b; de Vries *et al.*, *under review b*). These aspects are calibrated differently between individuals, depending on accumulated learning experiences throughout one's life course (Sobal *et al.*, 2006), and can similarly vary along a sociodemographic gradient. For instance, (implicit) liking and frequency of consuming (low-calorie) fruits tend to correlate negatively with income and education levels (Pechey *et al.*, 2015). Therefore, individuals (and subpopulations) with a high affinity and familiarity with high-calorie foods would presumably showcase the greatest expression of the high-calorie spatial memory bias, due to supporting contributions from these processes. By the same token, those with more positive learned associations and greater exposure to low-calorie alternatives would likely be able to "mask" the inherent spatial recall advantage of energy-dense foods and fall on the lower end of the bias spectrum.

In closing, foraging adaptations that evolved during our extended history as hunter-gatherers seemingly persist and exert an influence on how we navigate evolutionary-novel calorie-laden food landscapes today. Our results posit that embedded within our cognitive architecture is a calorie-sensitive spatial prioritization mechanism that once formed part of a successful foraging strategy, but now detrimentally leads us to purchase high-calorie snack foods habitually, visit high-calorie food outlets, and accumulate body weight. However, an improved ability to appropriately modify responses to high-calorie foods can help mitigate the bias' harmful dietary effects.

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Chapter 5

Appendix

Table A5.1.

Sociodemographic characteristics of participant samples across the two online test sessions.

Sociodemographic Characteristic	Test Session 1 ^a (N = 405)	Test Session 2 ^a (N = 316)
Sex (% Male)	56.7	57.9
Age (years)	47.57 (± 17.48) Range: 18 - 86	47.37 (± 17.64) Range: 18 - 86
Ethnicity (% Caucasian)	98.8	98.4
Education (%)	None or primary education: 0.5 Pre-vocational secondary education: 4.7 Theoretical pre-vocational secondary education: 17.3 Middle-level applied education: 25.9 Higher general or scientific education: 13.8 University of applied sciences (propaedeutic): 3.0 University of applied sciences (bachelor): 13.6 University of applied sciences (master): 0.3 University propaedeutic: 2.0 University bachelor: 2.5 University master/ doctoral/ postdoctoral: 16.5	None or primary education: 0.6 Pre-vocational secondary education: 5.1 Theoretical pre-vocational secondary education: 18.4 Middle-level applied education: 25.6 Higher general or scientific education: 14.6 University of applied sciences (propaedeutic): 2.8 University of applied sciences (bachelor): 13.0 University of applied sciences (master): 0.3 University propaedeutic: 1.9 University bachelor: 2.8 University master/ doctoral/ postdoctoral: 14.9
Income (%)	Minimum: 3.7 Below the national average: 16.3 Approximately the national average: 22.2 1 to 2 times the national average: 24.2 2 or more times the national average: 11.1 Missing: 22.5	Minimum: 3.5 Below the national average: 15.8 Approximately the national average: 21.2 1 to 2 times the national average: 25.9 2 or more times the national average: 11.1 Missing: 22.5
Occupation (%)	Employed: 67.9 Unemployed: 32.1	Employed: 67.1 Unemployed: 32.9
Subjective SES ^b	6.79 (± 1.40) Range: 1 - 10	6.79 (± 1.38) Range: 2 - 10
Neighborhood SES ^c	-0.05 (± 1.18) Range: -5.66 - 2.25	-0.08 (± 1.19) Range: -5.66 - 2.25

^a Test session 1 investigated food spatial memory; Test session 2 investigated behavioral outcomes.^b 10-point scale (Adler *et al.*, 2000)^c Z-distributed neighborhood SES scores (SCP Statusscores, 2017)

Table A5.2.

Characteristics of high- and low-calorie food images used in the spatial memory task.

Spatial Memory Task	Parameter (unit)	High-calorie M (SD)	Low-calorie M (SD)	p
Nutritional Content	Energy density (kcal/100g)	382.3 (106.9)	28.5 (15.7)	<.001
	Total energy displayed (kcal)	685.2 (797.5)	181.6 (310.4)	.006
	Protein to Carbohydrate and Fat Ratio	0.2 (0.2)	0.6 (0.8)	.178
Subjective Ratings	Perceived calories (mm) ^a	75.3 (16.1)	23.1 (15.8)	<.001
	Perceived healthiness (mm) ^a	23.5 (18.5)	79.6 (15.4)	<.001
	Recognizability (%) ^b	97.9 (2.1)	96.7 (5.5)	.534
	Subjective Complexity (mm) ^b	29.4 (6.6)	27.7 (4.1)	.331
Image Characteristics ^b	Color (Red; pixels)	0.5 (0.04)	0.5 (0.1)	.499
	Color (Blue; pixels)	0.2 (0.03)	0.2 (0.1)	.977
	Color (Green; pixels)	0.3 (0.02)	0.4 (0.1)	.496
	Size (pixels)	0.3 (0.1)	0.3 (0.1)	.850
	Brightness (luminance)	32.9 (9.0)	34.5 (12.5)	.711
	Contrast (luminance)	48.7 (9.9)	48.8 (12.5)	.983
	Complexity (pixels)	0.1 (0.02)	0.1 (0.04)	.805
	Normalized Complexity (pixels)	0.2 (0.1)	0.3 (0.1)	.496

^a Pilot results from a separate participant sample (de Vries *et al.*, 2020).

^b Data available from the *Food Pics* database (Blechert *et al.*, 2014)

Food Environment Questionnaire

Instructions: For each of the locations below, choose how often you have visited this location in **the past month** to **eat food** or **buy food**.

<i>Never</i>	<i>1x per month</i>	<i>2-3x per month</i>	<i>1x per week</i>	<i>2-3x per week</i>	<i>4-5x per week</i>	<i>6-7x per week</i>
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- ☐ Supermarket ^a
- ☐ Pastry shop (patisserie) ^b
- ☐ Mini supermarket ^a
- ☐ Department store ^a
- ☐ Discounters ^a
- ☐ Kiosk ^b (at the train/bus station)
- ☐ Gas station ^{a,b}
- ☐ Toko (traditional Asian supermarket or shop)
- ☐ Bakery ^b
- ☐ Food bank
- ☐ Market
- ☐ Delivery/ take-away ^a
- ☐ Grillroom/shoarma ^{a, b}
- ☐ Snackbar/Fastfood outlet ^{a,b}
- ☐ Restaurant ^a
- ☐ Cafeteria (at school/work)
- ☐ Delicatessen shop ^a
- ☐ Vegetable or fruit shop
- ☐ Butcher
- ☐ Fish seller
- ☐ Cheese shop ^b
- ☐ Reform store ^a
- ☐ Chocolate shop ^{a,b}
- ☐ Nuts shop ^b
- ☐ Sweets (confectionary) store ^{a, b}
- ☐ Ice cream shop ^b
- ☐ Pie or tart shop ^b
- ☐ Lunchroom/coffee company ^a
- ☐ Café
- ☐ Cupcake/muffin shop ^b
- ☐ Country/farm shop

^a Specific examples of store type in the Netherlands were mentioned.

^b Classified as a high-calorie food environment.

Table A5.3.

Predicting routine frequency of high-calorie snack consumption from the high-calorie bias in spatial memory.

Variable	B	95% CI	Beta	t	p	R	R ²
Model 1:							
Main effect of the high-calorie spatial memory bias							
Constant	-0.03	-2.53 – 2.47		-0.02	.983	.329	.108
Sex ^a	0.32	-0.11 – 0.76	0.08	1.46	.146		
Age	0.02	0.01 – 0.04	0.22	3.68	.000*		
Ethnicity	0.12	-1.04 – 1.28	0.01	0.20	.840		
Objective SES	-0.31	-0.64 – 0.03	-0.11	-1.79	.074		
Subjective SES	0.02	-0.14 – 0.17	0.01	0.22	.829		
Neighborhood SES	-0.02	-0.20 – 0.17	-0.01	-0.16	.875		
Liking High – Low Calorie	0.01	-0.02 – 0.03	0.05	0.48	.632		
Desirability High – Low Calorie	0.001	-0.02 – 0.02	0.01	0.12	.904		
Familiarity High – Low Calorie	0.34	-0.45 – 1.14	0.08	0.85	.394		
Importance of Convenience	0.40	0.03 – 0.78	0.12	2.12	.035		
Snack Purchasing Habit Strength	0.34	0.08 – 0.60	0.16	2.61	.010*		
Healthy Eating Intentions	-0.01	-0.22 – 0.20	-0.01	-0.08	.938		
Inhibitory Control ^b	-0.52	-4.65 – 3.60	-0.25	-0.25	.803		
High-calorie Spatial Memory Bias ^c	0.001	-0.001 – 0.003	0.05	0.92	.361		
Model 2: Interaction effects between the high-calorie spatial memory bias and psychological factors							
Constant	1.71			1.75	.082	.336	.113
Sex ^a	0.33	-0.10 – 0.77	0.09	1.50	.135		
Age	0.03	0.01 – 0.04	0.23	3.74	.000*		
Ethnicity	0.13	-1.04 – 1.31	0.01	0.23	.822		
Objective SES	-0.27	-0.61 – 0.08	-0.09	-1.51	.133		
Subjective SES	0.02	-0.15 – 0.17	0.01	0.18	.855		
Neighborhood SES	-0.01	-0.20 – 0.17	-0.01	-0.13	.901		
Liking High – Low Calorie	0.01	-0.02 – 0.03	0.05	0.46	.643		
Desirability High – Low Calorie	0.002	-0.02 – 0.02	0.02	0.21	.838		
Familiarity High – Low Calorie	0.31	-0.50 – 1.11	0.07	0.75	.454		
Importance of Convenience	0.39	0.01 – 0.77	0.12	2.02	.044		
Snack Purchasing Habit Strength	0.35	0.09 – 0.61	0.16	2.64	.009*		
Healthy Eating Intentions	-0.03	-0.24 – 0.19	-0.01	-0.25	.807		
Inhibitory Control ^b	-0.63	-4.80 – 3.54	-0.02	-0.30	.766		
High-calorie Spatial Memory Bias ^c	0.001	-0.001 – 0.003	0.05	0.80	.423		
HC SMB*Snack Purchase Habit	0.00	-0.002 – 0.003	0.02	0.30	.766		

HC SMB*Importance Convenience	0.002	-0.002 – 0.01	0.06	1.04	.299
HC SMB*Inhibitory Control	-0.001	-0.03 – 0.03	-0.003	-0.05	.964
HC SMB*Healthy Eating Intentions	0.00	-0.003 – 0.002	-0.02	-0.30	.764

^aMales are the reference group.

^bRate of commission errors in food-specific go/no-go task (Higher scores denote a *lower* inhibitory control to high-calorie foods).

^c $D_{\text{High Calorie}} - D_{\text{Low Calorie}}$ [HC SMB] (Lower values denote a *greater* bias in spatial memory for high-calorie foods).

*Significant at $\alpha_{\text{adjusted}} = .017$ (two-tailed).

Table A5.4.

Predicting routine visits to high-calorie food environments from the high-calorie bias in spatial memory.

Variable	B	95% CI	Robust SE	<i>t</i>	<i>p</i>
Model 1: Main effect of the high-calorie spatial memory bias					
Constant	0.07	-1.30 – 1.45	0.70	0.11	.916
Sex ^a	-0.02	-0.15 – 0.11	0.06	-0.31	.760
Age	0.01	-0.002 – 0.01	0.004	1.30	.193
Ethnicity	0.41	-1.02 – 1.83	0.72	0.56	.577
Objective SES	0.13	-0.02 – 0.28	0.08	1.71	.089
Subjective SES	-0.01	-0.08 – 0.06	0.03	-0.29	.770
Neighborhood SES	-0.003	-0.08 – 0.07	0.04	-0.09	.932
Liking _{High – Low Calorie}	-0.01	-0.01 – 0.002	0.004	-1.51	.133
Desirability _{High – Low Calorie}	0.003	-0.003 – 0.01	0.003	1.04	.301
Familiarity _{High – Low Calorie}	0.08	-0.20 – 0.36	0.14	0.56	.579
Importance of Convenience	-0.13	-0.27 – 0.01	0.07	-1.81	.071
Snack Purchasing Habit Strength	0.11	-0.02 – 0.24	0.07	1.70	.090
Healthy Eating Intentions	-0.01	-0.09 – 0.08	0.04	-0.13	.895
Inhibitory Control ^b	2.21	-2.46 – 6.88	2.37	0.93	.352
High-calorie Spatial Memory Bias ^c	0.00	0.00 – 0.001	0.00	1.14	.255
Model 2: Interaction effects between the high-calorie spatial memory bias and psychological factors					
Constant	-0.04	-1.25 – 1.18	0.62	-0.06	.951
Sex ^a	-0.02	-0.14 – 0.11	0.06	-0.25	.805
Age	0.01	-0.001 – 0.01	0.004	1.56	.119
Ethnicity	0.38	-0.97 – 1.73	0.69	0.56	.578
Objective SES	0.13	-0.01 – 0.28	0.08	1.78	.076
Subjective SES	-0.01	-0.07 – 0.06	0.03	-0.25	.802
Neighborhood SES	-0.004	-0.08 – 0.07	0.04	-0.10	.918
Liking _{High – Low Calorie}	-0.01	-0.01 – 0.01	0.004	-1.42	.158
Desirability _{High – Low Calorie}	0.004	-0.22 – 0.33	0.003	1.18	.241

Chapter 5

Familiarity ^a High – Low Calorie	0.05	0.02 – 0.26	0.14	0.37	.713
Importance of Convenience	-0.13	-0.26 – 0.003	0.07	-1.92	.056
Snack Purchasing Habit Strength	0.14	-0.26 – 0.003	0.06	2.22	.027
Healthy Eating Intentions	-0.01	-0.10 – 0.07	0.04	-0.29	.773
Inhibitory Control ^b	1.94	-0.61 – 4.48	1.29	1.50	.136
High-calorie Spatial Memory Bias ^c	0.001	0.00 – 0.001	0.00	1.57	.117
HC SMB* Snack Purchase Habit	0.001	1.98×10^{-5} – 0.002	0.00	2.02	.045
HC SMB*Importance Convenience	0.00	-0.001 – 0.001	0.00	0.85	.395
HC SMB*Inhibitory Control	-0.02	-0.03 – -0.003	0.01	-2.38	.018*
HC SMB*Healthy Eating Intentions	0.00	-0.001 – 0.001	0.00	-0.35	.730

^aMales are the reference group.

^bRate of commission errors in food-specific go/no-go task (Higher scores denote a *lower* inhibitory control to high-calorie foods).

^c $D_{\text{High Calorie}} - D_{\text{Low Calorie}}$ [HC SMB] (Lower values denote a *greater* bias in spatial memory for high-calorie foods).

*Significant at $\alpha_{\text{adjusted}} = .017$ (two-tailed).

Table A5.5.

Predicting BMI from the high-calorie bias in spatial memory.

Variable	B	95% CI	Robust SE	<i>t</i>	<i>p</i>
Model 1: Main effect of the high-calorie spatial memory bias					
Constant	27.80	22.48 – 33.12	2.70	10.28	.000*
Sex ^a	-1.14	-2.21 – -0.07	0.54	-2.10	.037
Age	0.07	0.04 – 0.09	0.01	4.63	.000*
Ethnicity	-3.21	-6.20 – -0.22	1.52	-2.11	.035
Objective SES	-0.40	-1.20 – 0.39	0.40	-1.00	.321
Subjective SES	-0.25	-0.64 – 0.15	0.20	-1.23	.221
Neighborhood SES	0.28	-0.11 – 0.68	0.20	1.42	.157
Liking ^a High – Low Calorie	0.01	-0.04 – 0.05	0.02	0.23	.821
Desirability ^a High – Low Calorie	-0.02	-0.06 – 0.02	0.02	-0.87	.387
Familiarity ^a High – Low Calorie	0.38	-1.43 – 2.19	0.92	0.42	.679
Importance of Convenience	-0.06	-0.94 – 0.81	0.45	-0.14	.887
Snack Purchasing Habit Strength	1.25	0.53 – 1.97	0.36	3.44	.001*
Healthy Eating Intentions	-0.15	-0.59 – 0.30	0.23	-0.65	.516
Inhibitory Control ^b	-8.04	-14.55 – -1.53	3.31	-2.43	.016*
High-calorie Spatial Memory Bias ^c	-7.29×10^{-5}	-0.01 – 0.01	0.003	-0.03	.977

Model 2: Interaction effects between the high-calorie spatial memory bias and psychological factors

Constant	29.12	24.15 – 34.08	2.52	11.54	.000*
Sex ^a	-1.16	-2.23 – -0.09	0.54	-2.13	.034
Age	0.06	0.04 – 0.09	0.01	4.45	.000*
Ethnicity	-3.22	-6.53 – 0.09	1.68	-1.91	.057
Objective SES	-0.53	-1.35 – 0.30	0.42	-1.25	.213
Subjective SES	-0.20	-0.61 – 0.21	0.21	-0.94	.347
Neighborhood SES	0.28	-0.12 – 0.68	0.20	1.38	.170
Liking _{High – Low Calorie}	0.01	-0.04 – 0.05	0.02	0.32	.753
Desirability _{High – Low Calorie}	-0.02	-0.06 – 0.02	0.02	-0.84	.404
Familiarity _{High – Low Calorie}	0.23	-1.60 – 2.06	0.93	0.25	.802
Importance of Convenience	-0.11	-1.01 – 0.78	0.46	-0.25	.803
Snack Purchasing Habit Strength	1.25	0.55 – 1.94	0.35	3.53	.000*
Healthy Eating Intentions	-0.11	-0.55 – 0.33	0.22	-0.50	.619
Inhibitory Control ^b	-7.79	-20.44 – 4.86	6.43	-1.21	.226
High-calorie Spatial Memory Bias ^c	0.001	-0.01 – 0.01	0.003	0.28	.777
HC SMB* Snack Purchase Habit	-0.002	-0.01 – 0.01	0.004	-0.60	.552
HC SMB*Importance Convenience	0.002	-0.01 – 0.01	0.005	0.31	.759
HC SMB*Inhibitory Control	-0.02	-0.11 – 0.07	0.05	-0.41	.686
HC SMB*Healthy Eating Intentions	0.004	-0.002 – 0.01	0.003	1.42	.157

^aMales are the reference group.

^bRate of commission errors in food-specific go/no-go task (Higher scores denote a *lower* inhibitory control to high-calorie foods).

^c $D_{\text{High Calorie}} - D_{\text{Low Calorie}}$ [HC SMB] (Lower values denote a *greater* bias in spatial memory for high-calorie foods).

*Significant at $\alpha_{\text{adjusted}} = .017$ (two-tailed).

Table A5.6.Intercorrelations (r_s with $df = 316$) between all measured predictor and outcome variables.

	1	2	3	4	5	6	7	8
High-calorie Spatial Memory Bias^a		-0.11*	-0.02	0.11*	-0.09	-0.01	0.05	-0.04
Snack Purchasing Habit Strength			0.22**	0.15**	-0.33**	0.19**	0.12*	0.17**
Importance of Convenience				-0.01	-0.10	0.12*	-0.09	-0.004
Inhibitory Control^b					-0.09	0.01	-0.06	0.01
Healthy Eating Intentions						-0.05	-0.10	-0.14*
Routine High-calorie Snack Consumption Frequency							0.24**	0.07
Routine High-calorie Food Environment Visits								0.12*
BMI								

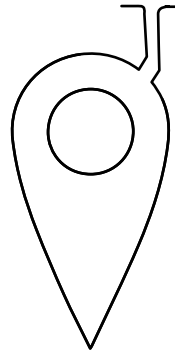
^a $D_{\text{High Calorie}} - D_{\text{Low Calorie}}$ (Lower values denote a *greater* bias in spatial memory for high-calorie foods).^b Rate of commission errors in food-specific go/no-go task (Higher scores denote a *lower* inhibitory control to high-calorie foods).* $p < .05$ (two-tailed); ** $p < .01$ (two-tailed)





Chapter 6

Human spatial memory is
biased towards high-calorie foods:
A cross-cultural online experiment



Abstract

Background: Human memory appears to prioritize locations of high-calorie foods, likely as an adaptation for foraging within fluctuating ancestral food environments. Importantly, this “high-calorie bias” in human spatial memory yields consequences for individual eating behavior in present-day food-abundant settings. However, as studies have mainly been conducted in European (Dutch) populations to date, we investigated whether the existence of the cognitive bias can be reasonably generalized across countries that vary on culturally-relevant domains, such as that of the USA and Japan. Furthermore, we probed sociodemographic factors that covary with the expression of the high-calorie spatial memory bias within different populations.

Methods: In an online experiment, we measured the food location memory of diverse participants from the USA (N=72; 44.4% Male; 54 \pm 15.99 years) and Japan (N=74; 56.8% Male; 50.85 \pm 17.32 years), using a validated computer-based spatial memory task with standardized images of high-calorie and low-calorie foods. To directly compare the magnitude of the high-calorie spatial memory bias in a broader cultural scope, we also included data from a previous online experiment that identically tested the food spatial memory of a Dutch sample (N=405; 56.7% Male; 47.57 \pm 17.48 years).

Results: Across distinct cultures, individuals more accurately recalled (i.e. displayed lower pointing errors for) locations of high-calorie foods versus that of low-calorie alternatives – regardless of hedonic preferences, familiarity with foods, and encoding times. The high-calorie bias in spatial memory was also expressed to a similar degree across diverse sociodemographic groups within a population.

Conclusions: Our results demonstrate that the high-calorie bias in spatial memory transcends sociocultural boundaries. Since the cognitive bias can negatively impact on our dietary decisions, it would be wise to invest in health promotion strategies that help to counter our seemingly universal capacity to efficiently (re)locate energy-dense foods.

Introduction

Essentially all organisms require energy from food to survive and reproduce (Pyke *et al.*, 1977). Many nutritional ecology models underlying individuals' eating behavior are thus based on the fundamental assumption that natural selection favored foraging strategies that maximize the rate of energy gain (Pyke *et al.*, 1977; Raubenheimer *et al.*, 2009; Schoener, 1971). Although evolved energy-efficient foraging mechanisms have long been recognized in various animal species – ranging from birds (Burke & Fulham, 2003; Cowie, 1977; Krebs, 1990; Sulikowski & Burke, 2007) to non-human primates (e.g. Cunningham & Janson, 2007; Janmaat *et al.*, 2014; Nakagawa, 2009) – the similar existence of foraging-related cognitive adaptations in humans has received less attention in literature (Krasnow *et al.*, 2011; New *et al.*, 2007b; Suarez *et al.*, 2019).

In a series of recent studies, we accumulated evidence consistent with the expression of a cognitive system in humans adapted for the efficient procurement of fitness-relevant nutritional resources. Across various experimental paradigms, we found that human memory shows sensitivity to the (relative) caloric “profitability” of a potential food, and more accurately recalls the locations of foods higher in energy density (de Vries *et al.*, 2020a; de Vries *et al.*, 2020b; see also New *et al.*, 2007b). The prioritization of high-calorie food locations in memory occurred independently of the sensory modality an individual used to explore food stimuli (i.e. vision versus olfaction), an individual's personal dietary preferences or familiarity with a food, and even one's conscious effort or explicit instruction to encode food locations (cf. de Vries *et al.*, 2020a). Importantly, this inherent “high-calorie bias” in human spatial memory yields consequences for how individuals navigate present-day obesogenic food environments, as an increased expression of the cognitive bias was found to predict a greater reported ease of locating high-calorie foods in a supermarket, more routine visits to high-calorie food retail locations (e.g. fast-food outlets), a stronger habit of purchasing high-calorie snack foods and a subsequently higher (less healthy) BMI (Allan & Allan, 2013; de Vries *et al.*, *under review a*; de Vries *et al.*, *under review b*). Thus, a cognitive mechanism that likely evolved as an adaptation for optimal foraging within fluctuating ancestral food environments, now maladaptively potentiates the selection and consumption of unhealthy high-calorie foods within our current food-abundant landscape.

However, as investigations have predominantly been conducted in European (Dutch) populations to date, it is less clear whether the existence of the high-calorie bias in spatial memory can be reasonably generalized to members of other countries. The evolutionary locus of the spatial processing bias strongly implies it to be a component of our universal cognitive architecture, thus its expression should be reliably observed across cultures (Krasnow *et al.*, 2011; Nairne, 2010; Tooby & Cosmides, 2005). Therefore, the present study set out to directly test this notion in two additional countries (i.e. USA and Japan) that diverge from one another on cultural domains relevant for food-specific spatial memory. Specifically, “Western” North American and “Eastern” Japanese cultures display different modes of cognitive processing, such as in the perception of visual objects and their contexts (Chua *et al.*, 2005; Kitayama *et al.*, 2003; Nisbett *et al.*, 2001), as well as the description of spatial relations between objects (Krasnow *et al.*, 2011; Mainwaring *et al.*, 2003). Relatedly, the physical layout of food environments deviates significantly between these countries, which may impact on the spatial reference system or perspective (e.g. reliance on landmarks) that individuals adopt, as well as the types of foods that individuals regularly consume (Ardilla, 1993; Pitt *et al.*, 2017; Mainwaring *et al.*, 2003; Montello, 1995). Finally, attitudes towards food and the assumed role food plays in daily life are known to vary cross-culturally: European individuals generally associate food most with pleasure, whereas American individuals generally emphasize the health (as opposed to hedonic) utility of food, and Japanese individuals tend to occupy an intermediate position on viewing food as either a medium for health or pleasure (Rozin *et al.*, 1999; see Werle *et al.*, 2013 for cultural differences in the “unhealthy food = tasty” intuition).

Given the behavioral and health implications of the high-calorie spatial memory bias, our secondary research objective was to identify potential “at-risk” subgroups within a population that showcase a marked expression of the bias. Literature increasingly suggests that dietary quality and BMI follow a sociodemographic gradient, in that individuals with a lower socioeconomic position (i.e. lower income, education, occupational status, or perceived social standing) generally exhibit poorer dietary patterns and a higher body weight (Adler *et al.*, 2000; Drewnowski *et al.*, 2014; Lakerveld *et al.*, 2015). The latter is often attributed to the fact that socially disadvantaged individuals tend to be exposed to less healthy physical food environments with an increased availability and accessibility to high-calorie foods (Ford & Dziewaltowski, 2008;

Larson *et al.*, 2009; Timmermans *et al.*, 2018). A novel explanation for how apparent structural differences in local food environments can give rise to dietary disparities between sociodemographic classes could involve systematic differences in the magnitude to which the high-calorie spatial memory bias is expressed and takes effect between groups. To explicitly assess this, we probed sociodemographic factors that covary with the expression of the high-calorie spatial memory bias within different populations.

Taken together, we hypothesized that:

H_{1A}: The high-calorie spatial memory bias is expressed across different cultures. Specifically, individuals within a country (i.e. USA and Japan) will display a greater overall accuracy in spatial memory for high-calorie foods compared to low-calorie alternatives – regardless of subjective evaluations and familiarity with foods.

H_{1B}: Sociodemographic factors moderate the expression of the high-calorie bias in human food spatial memory.

Methodology

Design

The present study had a two-by-two mixed factorial design with *Country* (USA versus Japan) as a between-subjects factor and *Caloric Density* (High versus Low) as a within-subjects factor. In an online experiment, participants had to complete food-specific spatial memory tasks and a series of questionnaires. The hypotheses, experimental design, and statistical analysis plan were preregistered, and are accessible with study data on the Open Science Framework database (Project URL: <https://osf.io/ptgda/>). For a final exploratory analysis, we included data from a previous online experiment that tested the food spatial memory of a Dutch sample in an identical manner (Project URL: <https://osf.io/nv7a9/> ; de Vries *et al.*, *under review a*). The latter was performed to directly compare the magnitude of the high-calorie spatial memory bias in a broader cultural scope (i.e. between American, Asian, and European populations; Rozin *et al.*, 1999). This study was approved by the Social Sciences Ethics Committee of Wageningen University.

Participants

Participants were a diverse sample of healthy adults (above the age of 18) from the USA and Japan, respectively. Individuals were recruited by the ISO-certified *Flycatcher* online research agency (www.flycatcher.eu), and excluded from participating

in the case of any self-reported illnesses or dietary restrictions, a current or medical history of eating disorders, or (total or partial) color blindness. A total of 121 individuals initially responded from the US population, but 43 (35.5%) participants did not fulfil one or more selection criteria (i.e. 20 (16.5%) self-reported poor health or a pre-existing health condition; 5 (4.1%) reported color blindness; 18 (14.9%) reported food restrictions), 5 (4.1%) dropped-out prior to the food spatial memory task, and 1 participant (0.8%) was removed due to poor response quality. A final sample of 72 individuals (44.4% Male; $M_{Age} = 54 (\pm 15.99)$ years, Range: 23 – 83 years) was thus obtained from the USA. With regards to the Japanese population, 191 panelists initially responded, with 116 (60.7%) individuals excluded at the beginning of the experiment on the basis of our selection criteria (i.e. 104 (54.5%) self-reported poor health or a pre-existing health condition; 1 (0.5%) reported color blindness; 11 (5.8%) reported food restrictions), and 1 (0.5%) dropped-out prior to the food spatial memory task. Thus, data from 74 individuals (56.8% Male; $M_{Age} = 50.85 (\pm 17.32)$ years, Range: 19 – 89 years) were collected for the Japanese sample. *A priori* power calculations for our confirmatory analyses (see <https://osf.io/ptgda/>) yielded a minimum number of 70 individuals to detect the high-calorie spatial memory bias within US and Japanese populations. Final participant samples of the two countries had similar sociodemographic distributions (**Table A6.1**). For our exploratory multi-country analysis, data pulled from the Dutch sample consisted of 405 individuals that fulfilled the same inclusion and exclusion criteria (56.7% Male; $M_{Age} = 47.57 (\pm 17.48)$ years, Range: 18 – 86 years; for details see de Vries *et al.*, *under review a*). After providing informed consent and completing the online experiment, participants were debriefed and financially compensated.

Procedure

Prior to testing, participants were provided with the general aim of the research, which was to investigate “*what people think about foods that are commonly found within the modern food environment*”. Participants first documented their sociodemographic characteristics (e.g. ethnicity, objective SES, and subjective SES) in a preliminary questionnaire. After, they rated their current hunger state and provided ratings on all (randomly-presented) food stimuli ($N=24$) on the parameters of *Liking*, *Desire to Eat*, and *Familiarity*. Individuals then completed the spatial memory task for both high- and low-calorie foods, with a five-minute break between caloric density

conditions. Finally, participants reported their height and weight, as well as answered questions on their healthy eating goals. The latter two questionnaires were presented in a counterbalanced manner (within each country), in order to minimize possible order effects on answers. The online test session took approximately 40 minutes to complete.

Apparatus and Stimuli

Food stimuli in spatial memory task. Images of high- and low-calorie foods were taken from the extended *Food Pics* database, which contains standardized pictures of Western, Asian, and Middle Eastern foods (Blechert *et al.*, 2019). Foods were considered “high-calorie” if they contained at least 225 kcal – and “low-calorie” if they contained at most 60 kcal – per 100 grams of food weight (cf. de Vries *et al.*, 2020b).

A set of 24 (unbranded) food pictures was used as stimuli for the spatial memory task, with 12 images of both high- and low-calorie items (de Vries *et al.*, *under review a*; de Vries *et al.*, *under review b*). The selection of final food images was modified differently for each country, based on results of a pilot study involving a separate sample of the target population in each country (N= 31 for the US sample and N= 29 for the Japanese sample; **Table A6.2**). For both countries, an equal number of sweet and savory foods were included across caloric density categories, to account for potential taste effects on spatial memory performance (de Vries *et al.*, 2020b; de Vries *et al.*, *under review b*). Furthermore, high-calorie stimuli showcased a greater energy density (kcal/100g) as well as total energy content (kcal) relative to low-calorie alternatives, and were correctly perceived as less healthy and to contain more calories (**Table A6.2**). On the other hand, high- and low-calorie foods were matched on macronutrient balance (i.e. protein to carbohydrate and fat ratios; Simpson & Raubenheimer, 2005), recognizability, and important perceptual characteristics (e.g. color and complexity) in the final stimuli sets of both populations (**Table A6.2**).

Spatial memory task. The computer-based spatial memory task was validated in diverse European samples as an instrument to measure food location memory accuracy (Allan & Allan, 2013; de Vries *et al.*, 2020b; de Vries *et al.*, *under review a*; de Vries *et al.*, *under review b*). Participants were first instructed to imagine that an international food market with 24 food stalls was taking place on an (unfamiliar) university campus. They were then shown 12 images of either high- or low-calorie foods, followed by an image of a map of the university campus with all 24 possible stall locations, at a fixed duration of three seconds each. After this initial viewing phase, the

location of the stall selling a food item was indicated on the campus map by a green crosshair, and this was consecutively done for all food stimuli within a caloric density condition ($N=12$). Individuals then rested for two minutes, after of which they had to perform a series of 12 spatial memory trials. On each trial, participants were randomly-presented with one of the previous food images and required to recall (via mouse-click) its correct assigned stall location on the campus map. All 24 possible stall sites were displayed anew each recall round, and participants could select the same stall location more than once, even though (correct) locations did not overlap between foods. Following a five-minute break, the spatial encoding and recall procedure was repeated for the remaining 12 foods of the other caloric density category. Food-location pairs within the campus map, as well as the order in which they were presented, were randomized uniquely for each participant. The order in which individuals completed the spatial memory task between caloric density conditions was counterbalanced within each country. Prior to the actual task with food images, participants first practiced encoding and recalling locations of non-food objects on the campus map, to familiarize themselves with the task paradigm. Importantly, the Japanese version of the spatial memory task (as well as administered questionnaires; *see below*) was translated using official language services, and the online experiment was piloted in a small separate sample ($N=3$) of native Japanese speakers for clarity and ease of comprehension, following successful internal pre-tests by the research agency.

Measurements

Primary outcome variables. The pointing error, or Euclidian distance (D) between correct and recalled stall locations, was averaged across all high- and low-calorie food stimuli to calculate an individual's spatial memory accuracy for high- and low-calorie foods, respectively (Allan & Allan, 2013; de Vries *et al.*, 2020b). As such, *lower* D scores indicate a *higher* accuracy in food spatial memory. The difference in spatial memory accuracy for high- versus low-calorie foods ($(D_{\text{High Calorie}} - D_{\text{Low Calorie}})$) of each individual was taken to represent the high-calorie bias in spatial memory. It follows that *lower* (negative) values denote an *increased* expression of the high-calorie spatial memory bias.

Predictor variables. Information on the sociodemographic variables of sex, age, ethnicity, objective SES (i.e. highest education level, annual household income, and occupation), and subjective SES (10-point MacArthur Subjective Social Status Scale;

Adler *et al.*, 2000) were collected (**Table A6.1**). Ethnicity was defined as the ethnic group an individual most strongly identifies with, and was coded into 7 possible categories for both populations: (1) White (2) Black/African/Caribbean (3) Asian (4) Latino (5) Arab (6) Other (7) Not Applicable (National Institutes of Health, 2015). Highest education level followed the national education classification system of a country, spanning from (1) elementary school to (6) university postgraduate for the US population, and from (1) lower secondary school to (8) university postgraduate for the Japanese population. Household income comprised of five categories, with (absolute gross) amounts adjusted for each country: (1) minimum, (2) below the national average, (3) approximately the national average, (4) one to two times the national average, and (5) two or more times the national average (**Table A6.1**). Occupation was classified into two groups across samples: (1) currently employed and (2) currently unemployed.

Control measures. Participants rated each food stimulus on Liking and Desire to Eat on a 100mm VAS (anchored from “Not At All” to “Very Much”), as well as Familiarity on a five-point scale (Tuorila *et al.*, 2001), given that hedonic evaluations and previous exposure to a food were shown to account for additional variation in food spatial memory accuracy (de Vries *et al.*, 2020a; de Vries *et al.*, 2020b; de Vries *et al.*, *under review b*). Similarly, hunger states were recorded at the onset of testing using a 100mm VAS (anchored from “Not At All” to “Very Much”).

As final (exploratory) checks, we required individuals to self-report their height (in *cm* or *feet*) and weight (in *kg* or *pounds*), in order to filter out any residual variance in food spatial memory performance attributable to BMI-related differences in (implicit) food attitudes or overall memory function (Czyzewska & Graham, 2008; Kanoski & Davidson, 2010; Loprinzi & Frith, 2018; Roefs and Jansen, 2002). Likewise, we asked participants to answer a Healthy Eating Goals questionnaire with two items (*In my daily life, I strive to eat healthy, It is important to me to eat healthy foods*) rated on a seven-point scale anchored from “Strongly Disagree” to “Strongly Agree”, as a measure of the importance they assigned to dietary self-regulation (Carver & Scheier, 2000; de Vries *et al.*, 2020b). The time a participant took to encode a food location (in *milliseconds*) during the cognitive task was also recorded, in order to effectively rule out a general learning account of differences in (spatial) memory performance – rather than a specific mnemonic effect of a food’s caloric content (de Vries *et al.*, 2020a; de Vries *et al.*, 2020b; de Vries *et al.*, *under review b*).

Data Analysis

Data was analyzed with IBM SPSS Statistics 25. Statistical significance was defined as $p < .05$. Food spatial memory data was analyzed using a linear mixed effects model (LMM), which represents a flexible and robust technique to model continuous data with correlated errors (Krueger & Tian, 2004). In the case of significant interaction effects, Fisher's LSD post-hoc tests were conducted.

The LMM fitting procedure made use of a backward stepwise approach. The covariance matrix of random effects in the saturated LMM (below) was established using Restricted Maximum Likelihood (REML) ratio tests and the -2 log likelihood (-2LL) test statistic. Next, the fixed part of the saturated LMM was simplified using Maximum Likelihood (ML) ratio tests and the -2LL test statistic. In both cases, the most parsimonious model was selected for and the final LMM was refitted with REML estimations. The finalized LMM was cross-checked with a forward stepwise modelling process and fulfilled all necessary assumptions. Income information was missing from a minority of participants (i.e. 8.3% and 2.7% from USA and Japan samples, respectively). Highly improbable BMI values of less than 13 kg/m² in 2 instances of the US sample – and less than 16 kg/m² in 1 instance of the Japanese sample (WHO Expert Consultation, 2004) – were also removed. However, LMM are generally robust to (conditionally) missing covariate data and the validity of estimated parameters in our final reported models was thus likely preserved (Graham, 2009; Schielzeth *et al.*, 2020).

Expression of the High-calorie Spatial Memory Bias Across Countries (H_{1A} and H_{1B}). To examine whether the high-calorie bias in human spatial memory generalizes across cultures (H_{1A}), we formulated a random intercept and slope LMM for each country ($N=2$), with main and interaction effects of *Caloric Density* and *Taste* as fixed factors, *Participant* and *Time* as random factors (covariance structure: Unstructured), *Sex*, *Age*, *Ethnicity*, *Education*, *Household Income*, *Occupation*, *Subjective SES*, *Liking*, *Desirability*, *Familiarity*, and *Hunger* as covariates, and *Spatial Memory Accuracy* (D) as the dependent variable.

To test for (country-specific) sociodemographic moderators of the bias (H_{1B}), we entered respective interactions between *Caloric Density* and all sociodemographic factors as additional fixed effects in the LMM of each population.

Moderation of Caloric Density Effects by Country (Exploratory). We combined data of the present study with that of a previous online experiment that

measured the food spatial memory of individuals from the Netherlands in an identical manner (de Vries *et al.*, *under review a*), to obtain sufficient power and test whether the magnitude of the high-calorie spatial memory bias differs across populations. We conducted a (random intercept and slope) LMM analysis on the combined dataset of 3 countries (i.e. USA, Japan, and the Netherlands), with main and interaction effects of *Country*, *Caloric Density* and *Taste* as fixed factors, *Participant* and *Time* as random factors (covariance structure: Unstructured), *Sex*, *Age*, *Ethnicity*, *Education*, *Household Income*, *Occupation*, *Subjective SES*, *Liking*, *Desirability*, *Familiarity*, and *Hunger* as covariates, and $\log_{10}(y+1)$ transformed *Spatial Memory Accuracy* (D) as the dependent variable. Since education classification systems differ per country, we standardized the categorization of Education into 7 possible levels, ranging from (1) primary education to (7) university postgraduate, following the International Standard Classification of Education (ISCED) guidelines (UNESCO Institute for Statistics, 2012).

We included individual interactions between *Caloric Density* and sociodemographic factors, to explore whether moderation effects would hold in a broader cultural context.

Results

The high-calorie bias in spatial memory was demonstrated across sociodemographic groups in the US sample.

Individuals in the US sample exhibited an average food spatial memory accuracy (i.e. average pointing error or D) of 316.64 pixels ($SD = 209.10$; Range = 0.68 – 1329.97).

The Caloric Density of a food was a significant (small-to-medium sized) predictor of how accurate its location was later recalled, $F(1,70) = 4.08$, $p = .047$, $\eta p^2 = 0.06$, 90%CI $\eta p^2 = [0.0004, 0.16]$, as individuals demonstrated lower pointing errors on average for locations of high-calorie foods relative to low-calorie alternatives (*Mean difference* = -99.23 pixels, 95% CI = [-197.19, -1.28]; **Figure 6.1**). The enhanced memory for high-calorie food locations was not due to sociodemographic characteristics, hunger state, food liking, wanting of a food, or familiarity with a food. Among tested covariates, spatial memory performance was also shown to be influenced to a larger degree by an individual's Ethnicity, in which Black/African/Caribbean individuals generally displayed larger pointing errors than those from Caucasian, Asian, and Latino ethnic groups (**Table A6.3**). Furthermore, final checks yielded a significant positive effect ($B = -0.003$) of encoding time – as well as negative effect ($B = 5.12$) of

BMI – on overall spatial memory accuracy, with similar sizes to that of Caloric Density (**Table A6.3**). However, none of these additional controls attenuated the effect of – or variation in food spatial memory accounted for by – Caloric Density, $F(1,68) = 4.26$, $p = .043$, $\eta^2 = 0.06$, $90\%CI \eta^2 = [0.001, 0.17]$. The spatial recall of a food did not depend on its Taste quality (i.e. sweet versus savory), $F(1,1583) = 0.37$, $p = .546$.

With regards to sociodemographic moderators, an initial trend was found for the interaction between Caloric Density and Education, $F(2,67) = 2.58$, $p = .083$, in which a higher education level tended to improve spatial memory performance for low-calorie foods only. However, this trend was eliminated upon controlling for individuals' BMI, $F(2,63) = 2.12$, $p = .128$. None of the remaining interactions proved to be significant, indicating that the high-calorie bias in spatial memory was equally expressed across sociodemographic groups in the US sample.

The high-calorie bias in spatial memory was specific to savory-tasting foods in the Japanese sample.

Individuals in the Japanese sample displayed an average food spatial memory accuracy of 322.05 pixels ($SD = 236.54$; Range = 0 – 1301.42), which mirrored the distribution of pointing errors in the US sample.

After controlling for sociodemographic variables, hunger, and respective food ratings, a significant but small interaction effect between Caloric Density and Taste on spatial memory performance was observed, $F(1,1584) = 4.06$, $p = .044$, $\eta^2 = 0.003$, $90\%CI \eta^2 = [0.0001, 0.01]$. Post-hoc (LSD) comparisons revealed that although individuals showcased lower pointing errors for high- versus low-calorie foods across Taste groups, the difference only reached significance for savory-tasting items (*Mean difference* = -40.41 pixels, $95\% CI = [-76.14, -4.68]$; **Figure 6.1**). In addition, food spatial memory improved to a similar degree with a higher rated Desirability of a food ($B = -0.59$), and females generally performed better than males (**Table A6.4**). On the other hand, neither BMI, reported nutritional intentions, nor encoding time predicted the accuracy of recalling food locations, as shown in final exploratory checks (all $p > .05$).

Finally, a significantly moderate interaction between Caloric Density and the sociodemographic variable of Occupation was observed, $F(2,69) = 3.24$, $p = .045$, $\eta^2 = 0.09$, $90\%CI \eta^2 = [0.002, 0.32]$, in which employed individuals displayed lower pointing errors for low-calorie foods relative to unemployed individuals (*Mean difference* = -90.93 pixels, $95\% CI = [-168.89, -12.96]$), $p = .023$. None of the remaining

interactions proved to be significant, indicating that locations of high-calorie foods were similarly prioritized (over that of low-calorie foods) across Japanese sociodemographic groups.

The magnitude of the high-calorie spatial memory bias was similar across US, Japanese, and Dutch populations.

In a combined exploratory analysis of the food spatial memory of individuals from the USA, Japan, and the Netherlands, a significant medium-sized main effect of Country was found, $F(2,548) = 25.08$, $p < .001$, $\eta^2 = 0.08$, 90% CI $\eta^2 [0.09, 0.22]$, as Dutch participants displayed overall lower pointing errors than both US (*Mean difference* = - 28.65% errors, 95% CI = [-18.71%, -38.58%]), $p < .001$, and Japanese samples (*Mean difference* = - 25.35% errors, 95% CI = [-15.61%, -35.09%]), $p < .001$. Spatial memory performance did not differ between US and Japanese participants, $p = .611$.

Controlling for general effects of Country, Caloric Density and Taste were shown to systematically predict food spatial memory accuracy to a small degree, owing to 3.11% lower pointing errors for high-calorie foods (95% CI = [-16.32%, -0.54%]; **Figure 6.1**), $F(1,552) = 4.44$, $p = .036$, $\eta^2 = 0.01$, 90% CI $\eta^2 [0.0003, 0.02]$, and 2.69% lower pointing errors for savory-tasting foods, $F(1,12177) = 6.89$, $p = .009$, $\eta^2 = 0.001$, 90% CI $\eta^2 [0.0001, 0.001]$, respectively. Importantly however, the interaction between Country and Caloric Density was not significant, $p = .349$, suggesting that the enhanced memory for high-calorie food locations was similar in magnitude across tested populations. Of the remaining covariates, a higher Education level ($B = -0.04$) and a higher rated Desirability of a food ($B = -0.001$) was associated with better spatial memory performance, whereas a male Sex and older Age ($B = 0.007$) predicted larger pointing errors, all with comparable effect sizes to Caloric Density (**Table A6.5**). Final checks revealed a further small influence of task (encoding) times ($B = -3.71 \times 10^{-6}$; **Table A6.5**), but this did not mitigate any of the aforementioned effects.

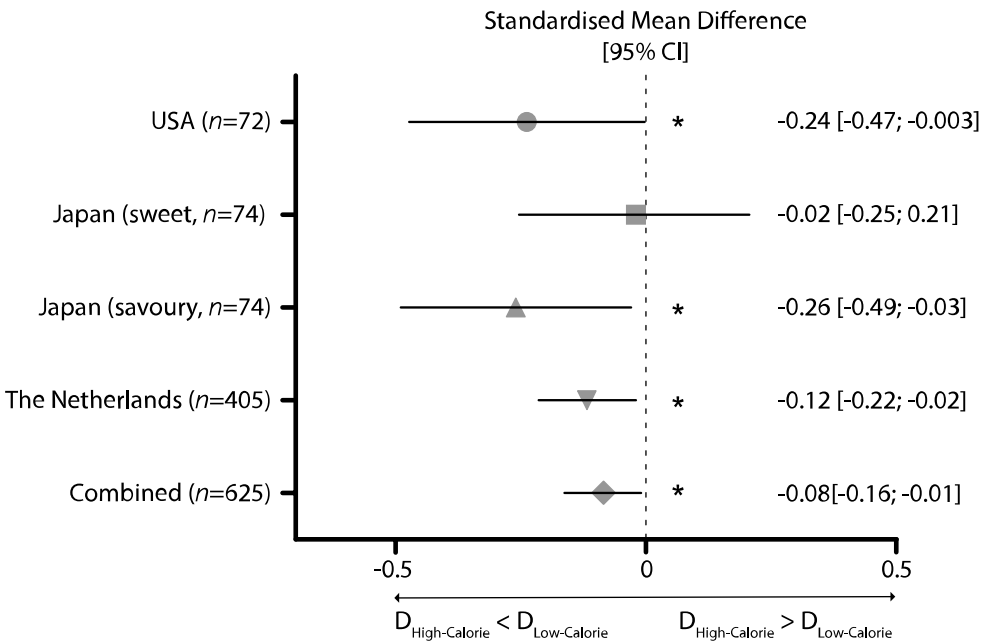


Figure 6.1. Standardized mean differences in spatial memory performance (D) for high-calorie versus low-calorie foods across populations. Lower (negative) values indicate a greater accuracy in spatial memory for high-calorie foods. A significant Caloric Density*Taste interaction was found in the Japanese sample, thus differences are stratified per Taste group. An asterisk denotes the significant expression of the high-calorie spatial memory bias within a population at $p < 0.05$.

Discussion

The present study utilized a cross-cultural online experiment to investigate the widespread existence of a bias in human spatial cognition for high-calorie foods. We found that individuals native to cultures varying on relevant cognitive characteristics, built food environments, and food attitudes were effectively identical in their food relocation performance: Locations of resources with a higher caloric quality were more accurately recalled than that of low-calorie alternatives to a similar degree across countries, regardless of individuals' hedonic preferences, familiarity with foods, or deliberate effort to encode food locations. The high-calorie bias in spatial memory was also uniformly expressed by diverse sociodemographic groups within a population. These results add empirical weight to the idea that the inherent spatial prioritization of high-calorie foods represents a component of our universal (human) cognitive architecture (New *et al.*, 2007b; de Vries *et al.*, 2020a; de Vries *et al.*, 2020b).

Cross-cultural comparisons provide a powerful yet previously unexplored tool to eliminate competing macro-level explanations for the mnemonic effect of caloric content on human spatial memory (e.g. culture-specific attitudes towards high-calorie foods), and our investigation shows first-hand that the cognitive bias transcends cultural boundaries (Lewis *et al.*, 2017; Nairne, 2010; Tooby & Cosmides, 2005). Though the spatial memory advantage of high-calorie foods was small in magnitude, a food's caloric density consistently accounted for a comparable amount of variation in pointing errors as general (reward-based) learning mechanisms (e.g. food desirability) across countries. Importantly, previous studies also established that a small one-unit (pixel) improvement in the relative memory accuracy for high-calorie food locations was sufficient to induce a subtle but significant change in eating behavior (e.g. 0.001 – 0.01 increase in BMI), after controlling for more explicit determinants such as an individual's reported healthy eating intentions (Allan & Allan, 2013; de Vries *et al.*, *under review a*; de Vries *et al.*, *under review b*). Taken together, results position a food's intrinsic nutritional properties as an ecologically-valid factor in the operations and behavioral consequences of human spatial cognition.

Our findings likewise imply that individual-level interventions aiming to reduce the *overall* expression of the cognitive bias to promote healthier dietary regulation would benefit from targeting other predictors of food spatial memory that are more likely under one's volitional control (e.g. reducing encoding time for high-calorie food locations by lowering the visual salience of high-calorie products). The same principle may be applied for minimizing social dietary inequalities: Training a higher desirability for healthier low-calorie items (e.g. fruits and vegetables) – which is especially compromised in socially disadvantaged groups (Pechey *et al.*, 2015) – can help to offset the underlying spatial recall advantage of energy-dense foods experienced across sociodemographic strata. Indeed, we found some support for such sociodemographic discrepancies in our Japanese sample, as unemployed individuals displayed systematically higher pointing errors for low-calorie foods relative to employed individuals. From a public health perspective, however, a more parsimonious and perhaps effective approach to support healthy eating behavior on both individual and group levels would be to limit the availability of high-calorie products, as well as high-calorie food locations (e.g. fast food outlets), in the immediate environment. Such structural modifications to the physical food environment would help to steer food

choice towards healthier alternatives, irrespective of individuals' responsiveness to proposed cognitive interventions (Hollands *et al.*, 2019; Pitt *et al.*, 2017).

That said, this study is not without its limitations. Firstly, our US and Japanese samples were not fully representative of respective adult populations at a national scale. Nevertheless, study samples had similar sociodemographic distributions and this allowed for a fair comparison of caloric density effects between cultures, which was our primary research interest. Moreover, one could argue that our resulting food images were still more "westernized" in nature, despite efforts to tailor them cross-culturally. The latter could have contributed to the initial Caloric Density-Taste interaction observed in our Japan analysis, as more contextually-appropriate items were available for our savory-tasting stimuli (e.g. ramen). We believe this speaks to a greater need for food image databases (e.g. Blechert *et al.*, 2019; Charbonnier *et al.*, 2016) to amplify existing efforts to diversify their collection of standardized pictures and increase cross-cultural applicability.

In closing, diverse sociodemographic groups from three distinct cultures were shown to display an identical food spatial memory "signature": individuals automatically prioritized in memory the locations of foods with a higher caloric content. Since the high-calorie bias in spatial memory can negatively impact on our dietary decisions, it would be wise to invest in health promotion strategies that help to counter our seemingly universal capacity to efficiently (re)locate energy-dense foods.

Acknowledgements

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Chapter 6

Appendix

Table A6.1.

Background characteristics of participant samples across cultures.

	USA (N = 72)	Japan (N = 74)
Sex (% Male)	32 (44.4%)	42 (56.8%)
Age (years)	54 (\pm 16) Range: 23 – 83	50.9 (\pm 17.3) Range: 19 – 89
Ethnicity (%)	White: 58 (80.6%) Black/African/Caribbean: 5 (6.9%) Asian: 4 (5.6%) Latino: 2 (2.8%) Other: 1 (1.4%) Not Applicable: 2 (2.8%)	White: 4 (5.4%) Asian: 69 (93.2%) Not Applicable: 1 (1.4%)
Education (%)	Elementary school: - Middle school: - High school: 36 (50%) Community College/Junior College: 6 (8.3%) University undergraduate: 17 (23.6%) University postgraduate: 13 (18.1%)	Lower secondary school: 6 (8.1%) Upper secondary general or vocational education: 19 (25.7%) Associate degree junior college: 1 (1.4%) Associate diploma college of technology: 5 (6.8%) Diploma professional training college: 2 (2.7%) Advanced diploma professional training college: 3 (4.1%) University undergraduate: 35 (47.3%) University postgraduate: 3 (4.1%)
Income (%)	Minimum: 8 (11.1%) Below the national average: 22 (30.6%) Approximately the national average: 26 (36.1%) 1 to 2 times the national average: 7 (9.7%) 2 or more times the national average: 3 (4.2%) Missing: 6 (8.3%)	Minimum: 6 (8.1%) Below the national average: 25 (33.8%) Approximately the national average: 18 (24.3%) 1 to 2 times the national average: 14 (18.9%) 2 or more times the national average: 9 (12.2%) Missing: 2 (2.7%)
Occupation (% Employed)	32 (44.4%)	50 (67.6%)
Subjective SES ^a	6 (\pm 2.0) Range: 2 – 10	5.28 (\pm 2.0) Range: 1 – 9
BMI	27.3 (\pm 5.5) Range: 18.4 – 51.1 Missing: 2 (2.8%)	22.0 (\pm 3.2) Range: 16.9 – 34.3 Missing: 1 (1.4%)

Healthy Eating Goals^b	5.3 (± 1.1) Range: 1 – 7	5.0 (± 1.3) Range: 1 – 7
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^a 10-point scale (Adler *et al.*, 2000).

^b 7-point scale (de Vries *et al.*, 2020b).

Table A6.2.

Characteristics of high- and low-calorie food stimuli used in the spatial memory task across cultures.

Spatial Memory Task - USA^a	Parameter (unit)	High-calorie M (SD)	Low-calorie M (SD)	p
Nutritional Content^b	Energy density (<i>kcal/100g</i>)	381.3 (111.7)	30.8 (16.1)	<.001
	Total energy displayed (<i>kcal</i>)	677.9 (797.8)	115.4 (112.1)	<.001
	Protein to Carbohydrate and Fat Ratio	0.2 (0.2)	0.4 (0.4)	.514
Subjective Ratings^c	Perceived calories (<i>mm</i>)	85.9 (19.6)	29.3 (23.3)	<.001
	Perceived healthiness (<i>mm</i>)	21.3 (23.6)	78 (24.2)	<.001
	Recognizability (%)	83.6 (6.7)	81.16 (6.7)	.381
Image Characteristics^b	Color (Red; <i>pixels</i>)	0.5 (0.03)	0.5 (0.1)	.796
	Color (Green; <i>pixels</i>)	0.3 (0.03)	0.4 (0.1)	.211
	Color (Blue; <i>pixels</i>)	0.2 (0.03)	0.2 (0.1)	.159
	Size (<i>pixels</i>)	0.3 (0.1)	0.3 (0.1)	.861
	Brightness (<i>luminance</i>)	33.3 (9.2)	31.5 (8.3)	.620
	Contrast (<i>luminance</i>)	48.2 (9.2)	45.2 (13.2)	.518
	Complexity (<i>pixels</i>)	0.1 (0.02)	0.1 (0.03)	.602
	Normalized Complexity (<i>pixels</i>)	0.3 (0.1)	0.3 (0.1)	.985

^a Food Pics catalogue numbers *High-calorie*: 2,4,16,27,53,60,103,104,116,134,286,517; *Low-calorie*: 199,233,250,251,260,364,389,392,413,442,453,466

^b Data available from the *Food Pics* database (Blechert *et al.*, 2019).

^c Pilot results from a separate sample of the target population (N = 31; 45.2% Male; M_{Age} = 51.5 (± 16.4) years, Range: 23 – 85 years)

Spatial Memory Task - Japan ^a	Parameter (<i>unit</i>)	High-calorie M (SD)	Low- calorie M (SD)	<i>p</i>
Nutritional Content ^b	Energy density (<i>kcal/100g</i>)	378 (109.1)	32 (16.3)	<.001
	Total energy displayed (<i>kcal</i>)	692.1 (788.5)	119.9 (109.1)	<.001
	Protein to Carbohydrate and Fat Ratio	0.2 (0.2)	0.3 (0.4)	.755
Subjective Ratings ^c	Perceived calories (<i>mm</i>)	80.8 (17)	41.8 (25.5)	<.001
	Perceived healthiness (<i>mm</i>)	36.4 (26.9)	73.9 (19.9)	<.001
	Recognizability (%)	91.1 (5.2)	91.7 (7.4)	.823
Image Characteristics ^b	Color (Red; <i>pixels</i>)	0.5 (0.03)	0.5 (01)	.729
	Color (Green; <i>pixels</i>)	0.3 (0.03)	0.4 (0.1)	.223
	Color (Blue; <i>pixels</i>)	0.2 (0.03)	0.2 (0.1)	.300
	Size (<i>pixels</i>)	0.3 (0.1)	0.3 (0.1)	.426
	Brightness (<i>luminance</i>)	37.1 (13)	30.6 (9.1)	.169
	Contrast (<i>luminance</i>)	49.5 (8.2)	46.1 (13.4)	.463
	Complexity (<i>pixels</i>)	0.1 (0.03)	0.1 (0.03)	.114
	Normalized Complexity (<i>pixels</i>)	0.3 (0.1)	0.3 (0.1)	.927

^a Food Pics catalogue numbers *High-calorie*: 2,4,16,27,53,60,103,116,134,286,517,619; *Low-calorie*: 199,233,250,251,260,333,389,392,413,442,453,466

^b Data available from the *Food Pics* database (Blechert *et al.*, 2019).

^c Pilot results from a separate sample of the target population (N = 29; 48.3% Male; M_{Age} = 48.6 (± 16.5) years, Range: 19 – 80 years)

Table A6.3.

Finalized linear mixed effects models (LMM) of food spatial memory performance of the US sample.

Variable	F	Df1	Df2	<i>p</i>	ηp^2	90%CI ηp^2
Model 1: Best-fitting LMM¹						
Intercept	59.95	1	65	<.001*	-	-
Caloric Density	4.08	1	70	.047*	0.06	0.0004 – 0.16
Taste	0.37	1	1583.2	.546	-	-
Ethnicity	2.47	5	65	.041*	0.16	0.02 – 0.63
Caloric Density*Education	2.58	2	67.4	.083	-	-
Model 2: Best-fitting LMM with exploratory covariates (i.e. BMI, Healthy Eating Goals, and Encoding Time)¹						
Intercept	2.74	1	59.5	.103	-	-
Caloric Density	4.26	1	67.8	.043*	0.06	0.001 – 0.17
Taste	0.26	1	1534.2	.612	-	-
Ethnicity	2.41	5	59.6	.047*	0.17	0.007 – 0.65
Caloric Density*Education	2.12	2	63.4	.128	-	-
BMI	6.25	1	59.6	.015*	0.09	0.01 – 0.23
Healthy Eating Goals	0.08	1	59.5	.779	-	-
Encoding Time	11.9	1	557.9	.001*	0.02	0.01 – 0.05

¹Dependent variable = Food spatial memory accuracy (*D*)

*Significant at $\alpha = 0.05$

Table A6.4.

Finalized linear mixed effects model (LMM) of food spatial memory performance of the Japanese sample.

Variable	F	Df1	Df2	<i>p</i>	ηp^2	90%CI ηp^2
Model 1: Best-fitting LMM (with and without exploratory covariates of BMI, Healthy Eating Goals, and Encoding Time)¹						
Intercept	297.79	1	128.1	<.001*	-	-
Caloric Density	2.00	1	70.1	.161	-	-
Taste	1.32	1	1584.2	.251	-	-
Desirability	7.63	1	1471.9	.006*	0.05	0.001 – 0.01
Sex	4.38	1	68.10	.040*	0.06	0.002 – 0.17
Caloric Density*Taste	4.06	1	1583.6	.044*	0.003	0.0001 – 0.01
Caloric Density*Occupation	3.24	2	69.03	.045*	0.09	0.002 – 0.32

¹Dependent variable = Food spatial memory accuracy (*D*)

*Significant at $\alpha = 0.05$

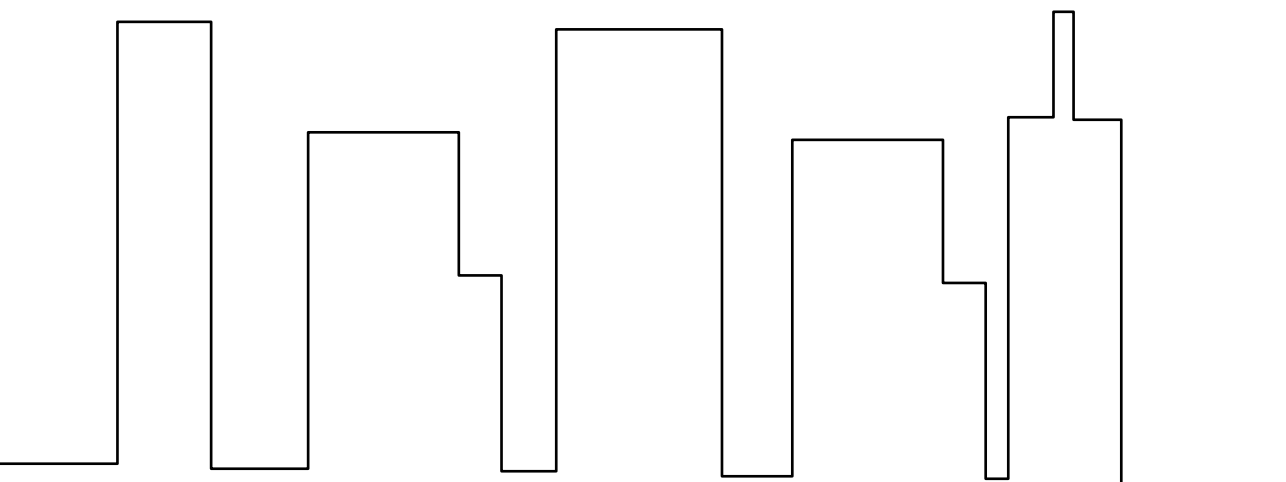
Table A6.5.

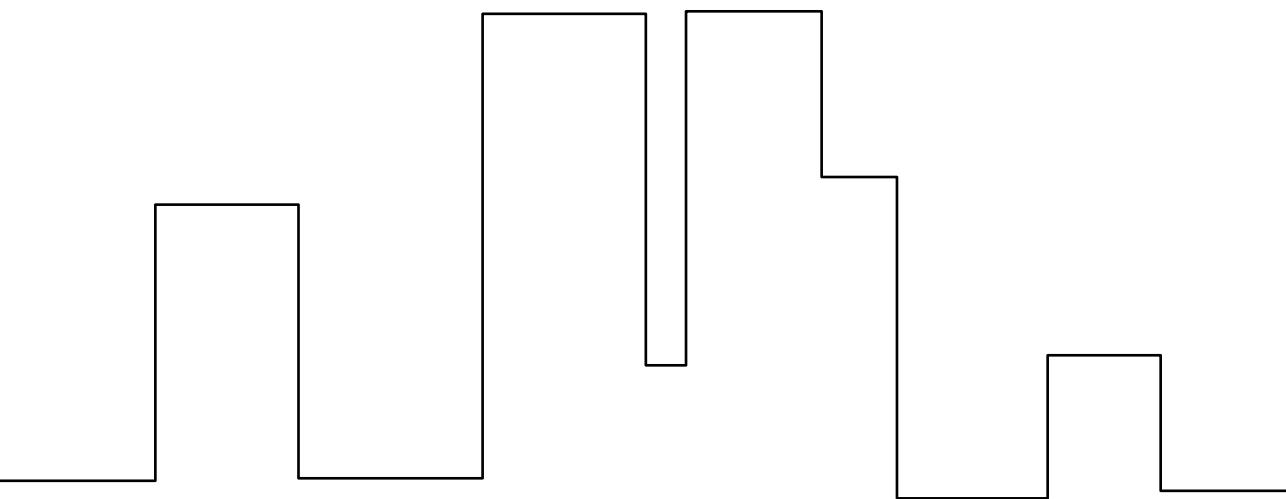
Finalized linear mixed effects models (LMM) of food spatial memory performance of the combined (i.e. USA, Japan, and the Netherlands) sample.

Variable	F	Df1	Df2	<i>p</i>	ηp^2	90%CI ηp^2
Model 1: Best-fitting LMM¹						
Intercept	488.7	1	556.2	<.001*	-	-
Country	25.08	2	548.1	<.001*	0.08	0.09 – 0.22
Caloric Density	4.44	1	552.1	.036*	0.01	0.0003 – 0.02
Taste	6.89	1	12177.3	.009*	0.001	0.0001 – 0.001
Sex	7.44	1	544.1	.007*	0.01	0.002 – 0.03
Age	45.89	1	544	<.001*	0.08	0.05 – 0.12
Education	14.41	1	544	<.001*	0.03	0.01 – 0.05
Desirability	5.97	1	11595	.015*	0.001	0.0001 – 0.001
Model 2: Best-fitting LMM with exploratory covariates (i.e. BMI and Task/Encoding Time)¹						
Intercept	205.59	1	543.1	<.001*	-	-
Country	27.13	2	544.9	<.001*	0.09	0.1 – 0.23
Caloric Density	4.36	1	548.3	.037*	0.01	0.0002 – 0.02
Taste	6.87	1	12103.2	.009*	0.001	0.0001 – 0.002
Sex	6.36	1	538.3	.012*	0.01	0.001 – 0.03
Age	43.92	1	538.8	<.001*	0.08	0.04 – 0.1
Education	11.76	1	538	.001*	0.02	0.01 – 0.05
Desirability	5.97	1	11498.5	.015*	0.001	0.0001 – 0.001
BMI	2.09	1	538	.148	-	-
Task (Encoding) Time	11.04	1	13034	.001*	0.001	0.0002 – 0.002

¹Dependent variable = Food spatial memory accuracy (*D*)

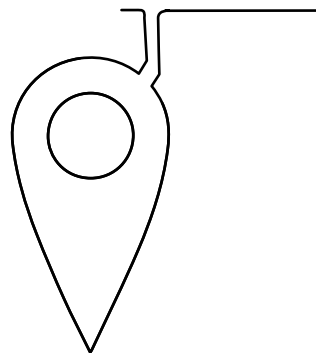
*Significant at $\alpha = 0.05$





Chapter 7

General Discussion



7.1 Aim and Main Findings

The modern food environment is characterized by the proliferation of cheap, convenient, and highly palatable energy dense foods, stimulating the (over)consumption of ‘unhealthy’ high-calorie items (Egger & Swinburn, 1997; Hill *et al.*, 2003; Lakerveld *et al.*, 2018). However, not everyone overeats and develops a positive energy balance, indicating that large differences exist in how individuals respond to the heightened systemic availability and accessibility of high-calorie foods (Swinburn *et al.*, 2011; Small, 2009; Wardle, 2007). Identifying the factors that underlie these individual differences has become an important research theme within the fields of human eating behavior and health psychology, and has significant implications for (public) health promotion efforts and expenditures (Kortt *et al.*, 1998; Swinburn *et al.*, 2011). This thesis is grounded on the novel premise that differences in the ability to successfully navigate current “obesogenic” settings may (partially) stem from a cognitive adaptation that evolved for optimal foraging within harsh ancestral food environments. Specifically, from the *graded* expression of a calorie-sensitive cognitive system that enabled ancestral humans to efficiently (re)locate valuable nutritional resources with varying spatiotemporal availabilities – a *bias* in spatial memory for high-calorie foods (Allan & Allan, 2013; New *et al.*, 2007b).

The overall aim of this thesis was to advance existing empirical observations on the presence and behavioral consequences of a high-calorie bias in human spatial memory (Allan & Allan, 2013; New *et al.*, 2007b). **Chapters 2, 3, and 6** primarily investigated the expression of the high-calorie bias in spatial memory across ecologically-valid sensory modalities (e.g. vision and olfaction), diverse sociodemographic groups within a population, and cultures that differ in cognitive processing characteristics and attitudes towards food. **Chapters 2, 4 and 5** were centrally focused on examining the potential translation of the cognitive bias into proximal (e.g. food search) and distal (e.g. BMI) – as well as incidental (e.g. grocery purchases) and routine (e.g. high-calorie food environment visits) – measures of individual eating behavior.

An overview of the main results of each chapter is provided in **Figure 7.1**. Through a series of lab-based, field-based, and online multisensory experimental paradigms, **Chapters 2 to 6** consistently demonstrate that human memory shows sensitivity to the caloric quality of foods, and automatically prioritizes the locations of

those with higher energy payoffs. Furthermore, findings confirm the maladaptive potential of the cognitive bias for individuals' eating behavior within a modern foraging context. A greater expression of the high-calorie bias in spatial memory predicted a lower perceived difficulty of finding high-calorie foods in a supermarket (**Chapter 4**), more routine visits to high-calorie food outlets (**Chapter 5**), stronger snack purchasing habits and a subsequently higher BMI (**Chapter 5**). This final chapter reflects on key conceptual insights and methodological features of the thesis, as well as addresses practical implications for health interventions and recommendations for future research.

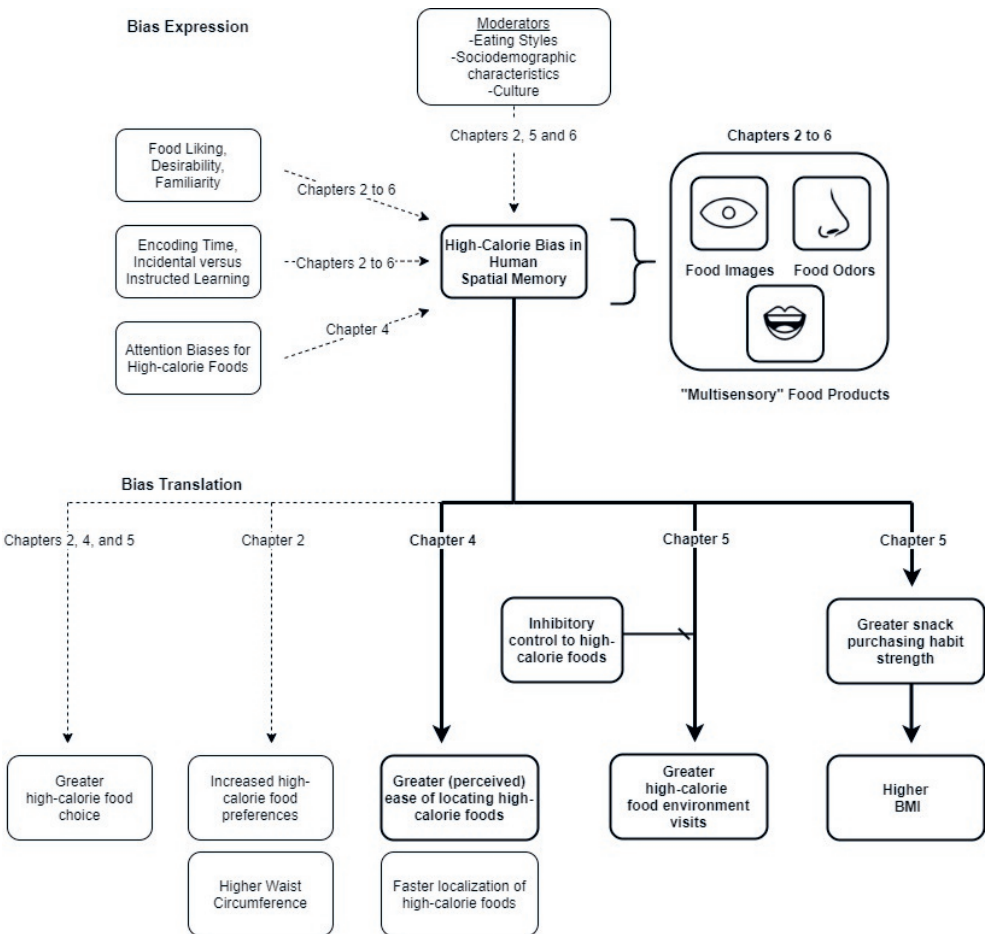


Figure 7.1. Synthesis of findings on the *expression* and *translation* of the high-calorie bias in human spatial memory. Relationships between boldened concepts (i.e. boldened unbroken lines) were found to be significant in at least one thesis chapter. A boldened line with a slanted end indicates a significant antagonistic effect.

7.2 Theoretical Reflections

In the following sections, I will reflect on this thesis' findings from a theoretical standpoint. I will first elaborate on aspects pertaining to the expression of the high-calorie bias in spatial memory (sections **7.2.1** and **7.2.2**), then pursue the bias' translation into dietary outcomes (sections **7.2.3** and **7.2.4**), and culminate with a commentary on how researching human spatial cognition and eating behavior in tandem has mutually benefitted both scientific domains (section **7.2.5**).

7.2.1 The high-calorie bias in human spatial memory is widely expressed, and bears the characteristics of an autonomous and efficient foraging-related mechanism.

Chapters 5 and 6 illustrate first-hand that members of varying cultures, as well as diverse sociodemographic groups within a population, all exhibit an enhanced memory for the locations of high-calorie foods to a similar degree (**Figure 7.1**). These results are compatible with the notion that the high-calorie bias in spatial memory represents a component of our universal (human) cognitive architecture (Krasnow *et al.*, 2011; Nairne, 2010; Tooby & Cosmides, 2005). Central to the explanation of a potential cognitive adaption, however, is a careful examination of its complex functional design, which enabled it to solve a particular adaptive problem in our evolutionary past (Cosmides & Tooby, 1997; Tooby & Cosmides, 2005). A complete description of the underlying properties of the high-calorie bias in spatial memory will also better inform intervention strategies that could target its activity in an effort to promote healthier diets (see sections **7.4** and **7.5.1**). Apart from showing sensitivity to the (relative) caloric content of a potential food, two principal functional features of the high-calorie spatial memory bias emerged from our investigations:

Firstly, the high-calorie bias in human spatial memory was found to develop outside of an individual's conscious effort (i.e. encoding times; **Chapters 2, 4, and 6**) or explicit instruction (**Chapter 3**) to encode food locations. Relatedly, individuals showcased an enhanced memory for high-calorie food locations regardless of their reported dietary preferences (e.g. Liking, Desirability; **Chapters 2 to 6**), previous exposure to foods (i.e. Familiarity; **Chapters 2 to 6**), deliberated nutritional intentions (e.g. Healthy Eating Goals; **Chapters 2 and 6**), or the amount of attention they allocated to high-calorie foods (**Chapter 4**) (**Figure 7.1**). Importantly, food-specific biases in early- and late- components of attention, as measured in **Chapter 4**, can be considered more objective proxies of unconscious versus conscious appetitive

motivations towards high-calorie foods, respectively (Werthmann, 2014). Our observations thus align with a mechanism that has autonomy or automaticity built into its architecture, in that its execution does not depend on an individual's volitional control and occurs as soon as its triggering stimuli (i.e. high-calorie food cues) are encountered – the latter a hallmark of an “impulsive” (Type 1) cognitive process (Evans, 2008; Evans & Stanovich, 2013; Stanovich, 2009; Strack & Deutsch, 2004).

Moreover, **Chapters 2 to 6** demonstrate that the high-calorie spatial memory bias already manifests within a single isolated sensory modality (i.e. using food images or food odors; **Figure 7.1**), and **Chapter 3** in particular provides direct evidence that its expression is not altered by an increasing range of sensory cues. This strongly implies that the cognitive bias requires only a limited presence of sensory information to be fully operational, and speaks to a mechanism with a high processing efficiency in that the bias performs as effectively in situations with less available spatial (sensory) task resources (Eysenck & Calvo, 1992). However, we believe an important precondition for the overall workings of the high-calorie bias in spatial memory – which we accordingly piloted for in all our studies – is that extant sensory cues have to be sufficiently recognizable (or minimally familiar) to individuals. That is, in order for individuals to successfully gauge the energetic “profitability” of a food based on encountered sensory cues, they need to have had previous eating experiences with a food item (or closely similar analogues) and learned to associate information on caloric quality with its sensory properties (Myers, 2018; Schoener, 1971; Yeomans, 2006). It follows that the spatial processing bias is unlikely to discriminate between completely novel foods, unless the differential energy return rates of such foods are to be readily detected prior to ingestion (e.g. smelling fat content from a distance; Boesveldt & Lundström, 2014) or shortly after tasting (e.g. Smeets *et al.*, 2011).

Collectively, these characteristics closely resemble the performance signature of an evolved spatial system wired for optimizing habitual foraging efforts, as together they would have (1) enabled the effortless registration and prioritization in memory of the location of sensory cues signaling energy-rich nutritional resources, (2) supported the efficient navigation towards these high priority resources as they became available or valuable (e.g. ripe) with seasonal fluctuations, and (3) conferred the added advantage of freeing up limited attentional resources to be used in other fitness-relevant tasks (e.g.

avoiding predators, caring for vulnerable members) (Krasnow *et al.*, 2011; New *et al.*, 2007b; Schoener, 1971).

7.2.2 Distinct spatial adaptations are expressed for efficient energy attainment and protein balance.

Besides energy content, the Taste quality of a food also independently predicted how well its spatial position was later recalled, with locations of savory-tasting foods prioritized above that of sweet-tasting alternatives. We speculated that the latter could reflect a foraging adaptation for protein-rich resources, in light of the nutrient-signaling function of tastes (Breslin, 2013; Teo *et al.*, 2018; Yarmolinsky *et al.*, 2009). This was further informed by anthropological data showing that ancestral hunter-gatherers had relatively high nutritional protein demands, and major protein sources (i.e. mobile animal prey) were more difficult to successfully capture than carbohydrate-rich resources (i.e. immobile fruits) (Bird *et al.*, 2009; Cordain *et al.*, 2000). Indeed, protein balance is tightly regulated across animal species, and there is evidence that protein homeostasis in humans can be maintained by (implicit) cognitive processes (Griffioen-Roose *et al.*, 2012; Simpson & Raubenheimer, 2000).

Unlike the high-calorie spatial memory bias however, the savory-taste bias in human food spatial memory was observed in only four out of six studies (cf. **Chapters 2, 4, and 6**). The reason for the discrepancy in robustness between Caloric Density and Taste effects is unclear. One possibility concerns inconsistencies in the macronutrient balance of food stimuli between Taste groups. In **Chapter 3**, sweet- and savory-tasting items were unintendedly matched on macronutrient composition (i.e. protein to carbohydrate and fat ratios). Thus during this instance, foods were equivalent on the aspect of nutrient balance between Taste conditions, which would have eliminated the supposed fitness-advantage of a more accurate location memory for (protein-rich) savory-tasting resources (Breslin, 2013; Simpson & Raubenheimer, 2005; Yarmolinsky *et al.*, 2009). It must be noted though that in **Chapter 5**, an influence of Taste on spatial memory performance was absent despite a systematically higher protein to carbohydrate and fat ratio of savory-tasting foods. However, the latter may have resulted from a compromised power to detect a significant Taste effect, as the slight prioritization of savory food locations in memory became apparent later within a larger study sample (**Chapter 6**). It therefore seems that the savory-taste bias in spatial memory is responsive to a food's relative protein (to non-protein) content. Taken

together, results reinforce the importance of macronutrient balance (i.e. protein to carbohydrate and fat ratios) to the food choice trajectories of human and non-human species, and attest to the utility of optimal foraging models that adopt the regulation of nutrients (as opposed to energy) as a currency (Felton *et al.*, 2009; Simpson *et al.*, 2003; Simpson & Raubenheimer, 2005; Winterhalder, 1981).

7.2.3 Immediate effects of the high-calorie spatial memory bias are mainly on psychological processes preceding (incidental and routine) food choice.

Another replicated finding of this thesis was that, contrary to expectations, the high-calorie bias in human spatial memory does not *directly* translate into individuals' food choices (cf. **Chapters 2, 4, and 5; Figure 7.1**). Rather, **Chapter 4** saw that the bias can potentiate the future (incidental) choice of a high-calorie food *indirectly*, by manipulating the subjective ease of acquiring these options in one's immediate surroundings and exploiting individuals' propensities to prefer highly convenient foods during instances of decision-making (Furst *et al.*, 1996; Sobal *et al.*, 2006). **Chapter 5** places these results against a wider spatiotemporal background and elucidates the capacity of the high-calorie bias in spatial memory to foster stronger snack purchasing habits, as well as a greater routine frequency of visiting high-calorie food outlets (**Figure 7.1**). This similarly indicates that the bias may play a more downstream role in stimulating unhealthy routine high-calorie food choice, by either creating momentum for repeated calorie-dense food selections within certain contexts (Sobal *et al.*, 2006; Verplanken & Orbell, 2003), or regularly placing individuals in physical contexts that increase the likelihood of choosing a high-calorie item (Cardello, 1994; Meiselman, 2006; see inter-variable correlations in Table S6 of **Chapter 5**).

On that note, it must be reiterated that the modest changes induced by the spatial processing bias on perceived high- versus low-calorie search difficulty ($B = 0.04$), snack purchasing habit strength ($B = -0.001$), routine high-calorie food environment visits ($B = -0.02$), and BMI ($B = -0.001$ for an indirect effect and $B = -0.01$ for a direct effect in Allan & Allan, 2013), were for a one-unit pixel increase in the relative accuracy of recalling high-calorie food locations. However, these changes likely represent a systematic underestimation of the forecasted impact on these outcomes in practice, as standardized between-subject differences in the expression of the high-calorie spatial memory bias ranged from 67 pixels (**Chapter 4**) to 102 pixels (**Chapter 5**) across studies.

7.2.4 “Reflective” goal-oriented psychological processes are important for healthy dietary regulation and can protect against the high-calorie spatial memory bias’ maladaptive “impulsive” effects.

A final recurring theme of this thesis pertains to the predictive validity of an individual’s “reflective” goal-oriented psychological processes in determining healthy eating behavior, and the seemingly antagonistic dynamic between one’s controlled dietary regulation efforts and “impulsive” maladaptive responses the high-calorie bias in spatial memory translates into (Evans, 2003; Evans & Stanovich, 2013; Hofmann *et al.*, 2008; Strack & Deutsch, 2004). In a health-minded sample of participants, individuals’ reasoned intentions towards healthy eating proved to be the sole robust predictor of proximal (e.g. food choice) as well as distal (e.g. BMI) eating-related measures, whereas the high-calorie bias in spatial memory failed to exert any effects (see **Chapter 2; Figure 7.1**). This presented the first indication of possibly conflicting *and* competing roles of the high-calorie spatial memory bias versus more reflective (i.e. Healthy Eating Goals) precursors of eating behavior. The importance of goal-directed psychological constructs was further strengthened in **Chapter 5**, which also provided more concrete evidence for a dual-systems account of individuals’ routine dietary behavior involving the cognitive bias. **Chapter 5** saw that an enhanced ability to inhibit responding to high-calorie food stimuli was independently associated with a lower BMI, whereas stronger (bias-mediated) snack purchasing habits translated into a higher body weight (**Figure 7.1**). More interesting, however, was the observation that an individual’s inhibitory control directly interacted with the high-calorie bias in spatial memory to reduce the frequency of visits made to calorie-laden food environments (**Figure 7.1**). A noteworthy outgrowth of this dual-systems account is that, given one’s established motivation to maintain a healthy diet, the tendency of the bias to impair self-regulation efforts and assume greater control over eating behavior will be most pronounced under circumstances in which self-control resources are low (e.g. in a cognitively-taxing or emotionally-distressed state; Hofmann *et al.*, 2009; Hofmann *et al.*, 2008).

7.2.5 Insights into human eating behavior advance our theoretical understanding of human spatial cognition.

The focus so far has been on how the operations of human spatial memory can be used to rationalize our eating behavior. Indeed, literature is replete with reports on the influence of human memory – especially episodic and working memory – on

individuals' food choice and food intake (see Higgs & Spetter, 2018 and Higgs *et al.*, 2012 for a review). However, we wish to conclude this section by reflecting on the utility of the reverse relationship. We illustrate below how studying human eating behavior in this thesis has mutually advanced our theoretical understanding of human spatial cognition.

Traditional frameworks of human memory – including the faculty of spatial memory – largely argue for the primacy of “general-purpose” learning mechanisms, which do not differentiate between the types of information that are processed (Nairne, 2010; Nairne & Pandeirada, 2010; Tooby & Cosmides, 1992). In this view, the control of recall performance is delegated to the “match” or degree of overlap in cues present between encoding and retrieval contexts (Tulving & Thomson, 1973). It follows that mnemonic encoding techniques are those that create “elaborated” memory traces and generate multiple possible retrieval cues that will likely match those present in recall environments (Craik & Lockhart, 1972; Craik & Tulving, 1975). As such, modern memory theory is *content-insensitive* at its core, because it assumes that environmental aspects – as opposed to information content – determine the likelihood of correct recall (Nairne, 2010). Our findings on the widespread mnemonic effect of a food's caloric content challenge these conventional assumptions, and join an increasing literature base centered on the notion of adaptive memory, which advocates a more functional account of human memory that is *content-sensitive* and attuned to processing fitness-relevant information (Nairne, 2010; Nairne & Pandeirada, 2010).

That being said, this thesis far from condones the complete abandonment of a “blank-slate” perspective of human cognition in favor of a purely “nativist” one, in which our cognitive architecture predominantly consists of separate specialized problem-solving systems as is often championed by evolutionary psychology (Tooby & Cosmides, 2005). Rather, our work empirically substantiates a hybrid model of human (food) spatial memory, by acknowledging the mutually exclusive yet *equally* important roles that nutrition-sensitive and general learning mechanisms play in its operations. The latter becomes evident when comparing effect sizes of the main determinants of spatial recall performance across studies. Despite differences in sensory modalities, participant samples, and experimental procedures, a food's intrinsic Caloric Density (and Taste) consistently accounted for a comparable (unique) proportion of variance in spatial memory accuracy as its rated Liking, Desirability, and Familiarity, and even the

time an individual took to encode food locations within intentional learning paradigms (e.g. **Chapters 2 and 6**; see Haun *et al.*, 2006 for a similar interpretation of human spatial cognition).

7.3 Methodological Considerations

7.3.1 *Strength: Variety of studies included*

The methodological composition of this thesis strongly delivered on two major fronts. The first concerns the inclusion of a variety of experimental paradigms – encompassing lab-based, field-based, and online-mediated studies – to address a set of complementary research questions on the cognitive bias. The relevance of each study type for the specific aims of this thesis are elaborated on below.

The use of highly-controlled lab experiments in **Chapter 2** was conducive to obtaining rigorous evidence for the existence of food-specific biases in human spatial memory. This experimental format allowed us to simultaneously control for potential confounders (e.g. differences in encoding times), avoid floor or ceiling effects in our primary research objectives (e.g. by standardizing hunger state), effectively manipulate Caloric Density and Taste features of food stimuli, as well as isolate effects on spatial memory performance unique to the nutritional properties of a food (Falk & Heckman, 2009; Webster & Sell, 2007). These two beginning experiments also proved to be a crucial step in validating task materials (i.e. adapted computer-based spatial memory task, standardized food images and food odors) for use in remaining studies. By the same token, examining the expression of both the high-calorie spatial memory bias and high-calorie biases in visual attention in the lab in **Chapter 4** provided a robust test of whether their associations would be internally valid (Roe & Just, 2009).

After establishing a proof-of-concept in **Chapter 2**, our follow-up investigation within the field setting of **Chapter 3** was an ambitious test for the generalizability of the high-calorie bias in spatial memory to more “naturalistic” foraging circumstances. The methodological set-up of **Chapter 3** made it possible to (randomly) assign foods to dispersed locations in three-dimensional space and for individuals to spatially navigate between food stimuli. It also permitted the integration of an incidental learning procedure and the accommodation of a large and more heterogeneous sample of participants, which would have been difficult to achieve in our lab-based experimental paradigm. Relatedly, the semi-controlled supermarket setting in **Chapter 4** was not

only ecologically-valid for dissecting real-world eating behavior in a modern foraging context, but it similarly proved useful in detecting small changes in food search parameters that likely would have remained hidden in “noisier” natural field experiments (e.g. recording participant movements unobtrusively during peak supermarket hours; Harrison and List, 2004).

Finally, our online-mediated studies were instrumental to further demonstrating the external validity of the cognitive bias and its behavioral consequences across sociodemographic groups (**Chapters 5 and 6**), cultures (**Chapter 6**), and situational testing conditions, given that individuals were free to complete online experiments at a place and time of their choosing (**Chapters 5 and 6**). An online study format was particularly beneficial for giving us access to subpopulations (e.g. low socioeconomic position, overweight/obese individuals) and those native to a completely different culture, that otherwise would have been very challenging to reach using conventional recruitment methods (Reips, 2000; Wright, 2005). Importantly, stratified sampling based on sociodemographic variables (e.g. age, education level) was feasible in **Chapter 5**, which culminated in a nationally representative sample of our target Dutch population that we could draw study conclusions from.

7.3.2 Strength: Range of eating behavior measures

This thesis also featured a broad range of eating behavior measures, which varied on conceptually meaningful temporal (i.e. *proximal* to *distal* effects) and frequency (i.e. *incidental* to *routine* behavior) dimensions (**Figure 7.2**). In doing so, we covered a wide spectrum of possibilities in assessing behavioral targets of the high-calorie spatial memory bias. The pros and cons of each category of investigated outcomes are discussed below.

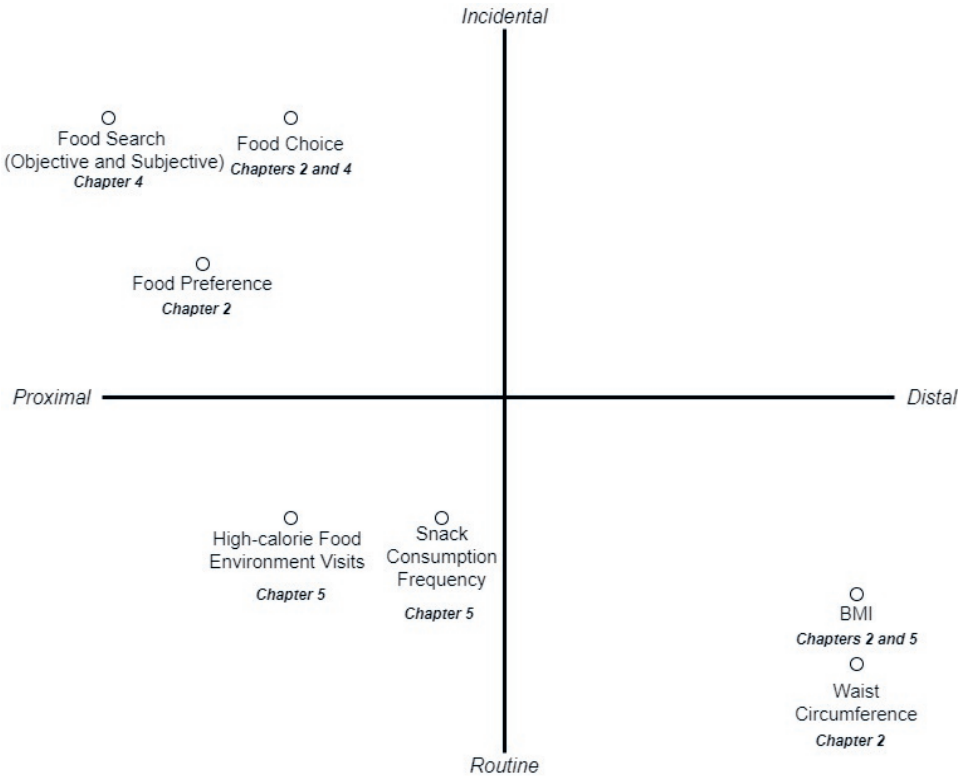


Figure 7.2. The collection of eating behavior measures featured in this thesis, which varied on temporal and frequency dimensions. The temporal (*proximal*–*distal*) axis refers to the position of a measure along the hypothesized behavioral chain of events triggered by the high-calorie spatial memory bias. The frequency (*incidental*–*routine*) axis reflects whether a measure denotes a single-instance or repeated form of eating behavior as operationalized in this thesis. As our distal measures only concerned individuals’ long-term eating behavior, incidental-distal variants were absent from this thesis.

Incidental and proximal markers of eating behavior (i.e. food preference and food choice) were employed in **Chapter 2** as a first exploratory step to gauge the bias’ effects. In light of the established association between the high-calorie bias in spatial memory and individual BMI (Allan & Allan, 2013), we reasoned that the latter could have resulted from a greater bias-induced tendency to prefer and prospectively choose for high-calorie foods more upstream in the behavioral pathway (Allan & Allan, 2013; Paradis *et al.*, 2009; Rothmund *et al.*, 2007; Stoeckel *et al.*, 2008). In addition, from a methodological standpoint, the Macronutrient and Taste Preference Ranking Task demonstrated good reliability and construct validity in previous investigations (de Bruijn *et al.*, 2017; de Vries *et al.*, 2018; de Vries *et al.*, 2019), and our lab-based food choice

measure enabled us to covertly record participant food selections (under the guise of a “performance prize”) while controlling for product availability and product placement aspects (Hollands *et al.*, 2019; van Kleef *et al.*, 2012). Outcomes of the same category were chosen in **Chapter 4** (i.e. objective and subjective food search times; high-calorie grocery purchases) based on the same theoretical grounds, but with the added methodological benefit of an ecologically-valid (physical) food navigation context. Despite possessing certain advantages, a notable caveat of incidental measures is that they capture one mere “snapshot” in time of an individual’s eating trajectory. As such, they may not accurately reflect one’s longitudinal dietary choices, which aggregate multiple timepoints and situations (Furst *et al.*, 1996; Sobal & Bisogni, 2009; Sobal *et al.*, 2006). On a related note, our incidental parameters lacked an appropriate situational backdrop to assess an individual’s default dietary decisions (e.g. by framing food choices as an experimental reward; Meiselman, 2006). This may have unduly impacted our results, as task instructions could have activated more deliberated or strategic processes during decision-making, when most food decisions are intuitive and heuristic in nature (Furst *et al.*, 1996; Köster, 2009; Sobal & Bisogni, 2009).

Therefore, we increasingly adopted more routine and contextually-diverse eating-related parameters, in order to approximate an individual’s habitual behavioral patterns as best as possible. **Chapter 5** included routine frequencies of (proximal) high-calorie snack consumption and high-calorie food environment exposure. We utilized a culture-specific snack FFQ for the former, which encompassed an exhaustive range of high-calorie snack foods commonly eaten in the Netherlands and was validated for use in the Dutch population (Streppel *et al.*, 2013). For the second routine-proximal measure, we developed a questionnaire to classify high-calorie food environments and calculate the frequency of (monthly) visits to them. Although our *Food Environment Questionnaire* has yet to be formally validated against individuals’ actual movements between food retail outlets (see section **7.5.2**), our classification system paralleled expert-derived “healthiness scores” of urban Dutch food outlet types (Timmermans *et al.*, 2018) and the questionnaire showed good usability in the study and its preceding pilot. Finally, routine and distal indicators of eating behavior (i.e. BMI and Waist Circumference; **Chapters 2 and 5**) were relevant to investigate for reasons of health and replicability (cf. Allan & Allan, 2013). Namely, both BMI and Waist Circumference serve as good objective anthropometric proxies of excess fat mass (Bouchard, 2007)

and dietary quality (Paradis *et al.*, 2009; Newby *et al.*, 2003; Newby *et al.*, 2004), albeit with differing sensitivities to (regional) adiposity (Stevens *et al.*, 2008). A disadvantage generally associated with distal outcomes is that they ultimately represent a product of a complex interplay of factors (i.e. energy expenditure in addition to energy intake), and are thus less “powered” to detect a hypothesized effect on, and limited in providing detailed mechanistic insights when used alone. Furthermore, a downside of our routine behavioral measures is that they mainly concerned self-reported questionnaires, which are susceptible to report biases due to social desirability effects (Hebert *et al.*, 1995; van de Mortel, 2008). However, self-reports presented the only feasible option for a large online study format, sufficient controls (e.g. anonymity and honesty reminders, question order randomization, data quality checks) were implemented to reduce the risk of biased responses.

7.3.3 Limitation: Spatial memory task variants

The first limitation of this thesis concerns the inclusion of only two spatial memory task variants, with the computer-based (two-dimensional map) version being the dominant means of measuring individual food spatial memory across studies (i.e. all but **Chapter 3**).

The computer-based food spatial memory task embodies a classic “table-top” paradigm to test object location memory (e.g. Pezdek *et al.*, 1986), and performance on the task was shown to previously covary with a conceptually-relevant marker of long-term dietary intake (i.e. BMI; Allan & Allan, 2013), as well as other (incidental and routine) eating-related parameters in this thesis (**Chapters 4 and 5; Figure 7.1**). However, an enhanced (computer-tested) memory for high-calorie food locations did *not* correlate with actual food search behavior in a larger supermarket setting, despite observing a faster localization of high- versus low-calorie foods in the latter (**Chapter 4; Figure 7.1**). As discussed in **Chapter 4**, this could be attributed to the fact that human spatial memory is a complex cognitive faculty, and distinct spatial systems – as well as distinct forms of spatial learning – are known to function at different scales and layouts of space (Hegarty *et al.*, 2006; McNamara & Shelton, 2003; Pazzaglia & Taylor, 2007; Piccardi *et al.*, 2010). Relatedly, variations in the availability of sensory (spatial) information for individuals to use in spatial tasks between navigational contexts could have contributed to this discrepancy (Wolbers & Hegarty, 2010). For instance, additional visual cues (e.g. product and aisle “landmarks”) were likely present in the supermarket, which could have

allowed for a richer construction of cognitive maps compared to the lab-based computerized task version (Downs & Stea, 2011; Wolbers & Hegarty, 2010).

As such, we cannot exclude the possibility that a partial dissociation exists between performance on the computer-based food spatial memory task and real-world food wayfinding behavior (for a similar conclusion see Hegarty *et al.*, 2006; but see **Chapter 3** and New *et al.*, 2007b for replication of the high-calorie spatial memory bias in a larger maze-like food setting and outdoor food market). A promising development in this regard concerns the use of virtual spatial navigation tasks, which can mirror the sensory complexity of three-dimensional environments (e.g. by incorporating odors; Radvansky & Dombeck, 2018) and closely approximates individuals' large-scale spatial ability (Cogné *et al.*, 2017; Ventura *et al.*, 2013). Virtual environments can also accommodate individual differences in spatial cognition (e.g. orientation ability and cognitive styles in spatial representation; Kozlowski & Bryant, 1977; Pazzaglia & Taylor, 2007), to better disentangle food navigation implications of the spatial processing bias.

7.3.4 Limitation: Participant populations

Finally, although this thesis investigated the expression and translation of the high-calorie spatial memory bias in varied sociodemographic and cultural groups (cf. **Chapters 5 and 6**), an adaptive account of the cognitive bias can be further corroborated by including more indigenous participant populations in future research efforts. Notably, to assess the generalizability of the spatial processing bias, we recruited samples from exclusively urbanized societies that have some diversity in spatial cognition (i.e. conceptualizing spatial object relations; Mainwaring *et al.*, 2003), but these cross-cultural variations were perhaps not substantial enough (Majid *et al.*, 2014). That is, language structures how individuals specify the locations of objects with respect to a reference object, and the dominant referencing style (or frame) between US English, Japanese, and even Dutch speakers is largely the same. Thus, given sufficient resources, the current evidence could be supplemented with food spatial memory data from certain indigenous tribal groups that practice a categorically different spatial relational language compared to post-industrialized societies (e.g. Haun *et al.*, 2006; Majid *et al.*, 2004). An additional advantage of studying this population is that modern hunter-gatherer tribes have an improved ability to name and discriminate between odor qualities (Majid & Kruspe, 2018; Wnuk & Majid, 2014), which would enable a more fair comparison of bias expression between sensory modalities (cf. **Chapters 2 and 3**).

7.4 Practical Implications for Health Interventions

Insights on the capability of the high-calorie bias in spatial memory to impinge on how individuals forage within present-day food settings – and the specific intermediary processes that are involved (**Figure 7.1**) – offer a new perspective for existing interventions that aim to stimulate healthier food navigation within obesogenic environments. Though not explicitly tested in this thesis, we distinguish between health promotion strategies that could effectively intervene at the overall expression of the high-calorie spatial memory bias, versus those that target a more downstream process and may thus directly mitigate the bias' translation into undesirable dietary outcomes.

Chapters 2, 3, 4, and 6 illustrate how the prioritization in memory of high-calorie food locations appears to operate autonomously and rapidly, which questions how susceptible the effect of caloric density on food spatial memory would be to attempts that aim to simply curtail it (e.g. via (re)training attentional allocation to low-calorie foods; Kemps *et al.*, 2014). Furthermore, the high-calorie bias in spatial memory requires minimal sensory information to be expressed (cf. **Chapters 2 and 3**), implying that the cognitive bias is likely to be triggered as soon as high-calorie food cues are perceived in one's surroundings. To remedy this construction on an individual level, one approach would be to focus on other – equally potent – determinants of human food spatial memory (see section **7.2.5** for discussion on effect sizes of determinants). That is, nutritional interventions intending to effectively counter (or “mask”) the underlying spatial prioritization of high-calorie foods could benefit from increasing individuals' hedonic valuations of – and familiarity with – healthy low-calorie items. Such interventions entail repeated taste exposures and reward-based conditioning strategies (e.g. flavor-consequence learning with fruits and vegetables; Appleton *et al.*, 2018; Yeomans, 2006). An advantage of this approach is that food preferences and food exposure can mutually reinforce one another over time (Birch, 1999; Corsini *et al.*, 2013), thus an individual's spatial memory for low-calorie foods can conceivably be enhanced using the same (smaller) set of techniques that *simultaneously* increase desirability and familiarity of low-calorie options.

In addition, drawing on findings from **Chapter 5**, two classes of behavior change strategies may be operationalized to disrupt the translation of the high-calorie spatial memory bias. Firstly, to resist bias-induced tendencies to visit high-calorie food outlets (**Figure 7.1**), individuals' ability to withhold responses to high-calorie foods can

be trained with the use of food-specific Go/No Go paradigms (Jones *et al.*, 2016; Veling *et al.*, 2017). Food Go/No Go training has been shown to moderately reduce hedonic valuations, choice and intake of no-go food items (e.g. snack foods), as well as facilitate short-term weight loss, in studies using both healthy-weight and obese populations (Chen *et al.*, 2018; Veling *et al.*, 2013). Notably, this approach may particularly be beneficial in instances when reflective self-control processes typically fail (e.g. Hofmann *et al.*, 2008; Hofmann *et al.*, 2009), as Food Go/No Go training is thought to strengthen a more automatized form of response inhibition (Littman & Takács, 2017; Veling *et al.*, 2017). Secondly, the capacity of the spatial processing bias to form or consolidate snack purchasing habits (**Chapter 5; Figure 7.1**) merits the consideration of behavior change strategies that integrate a contextual component with a behavioral one. The latter consists of techniques such as implementation intentions (e.g. “If I feel hungry on the way home from work, then I will buy an apple instead of chips at the train station”) and cue monitoring (e.g. feeling hungry on the way home from work cues me to purchase chips at the train station) (Abraham & Michie, 2008). Literature demonstrates that implementation intentions and cue-monitoring – especially when used in combination – represent a promising manner to reinforce healthy eating behavior (e.g. increase fruit and vegetable intake), as well as diminish existing unhealthy dietary habits (e.g. unhealthy snack consumption) (Adriaanse *et al.*, 2011; Michie *et al.*, 2009; Verhoeven *et al.*, 2014).

Alternatively, policy makers could opt for a more parsimonious structural approach to curb *both* the expression and translation of the high-calorie bias in spatial memory, by reversing the greater systemic availability and accessibility to unhealthy high-calorie items in our current food landscape (Lake & Townshend, 2006; Pitt *et al.*, 2017; Swinburn *et al.*, 2011). Strategically limiting the range and prominence of (ultra-processed) energy dense options in situational contexts where food decisions are regularly made (e.g. supermarkets) may prove useful in reducing the frequency with which the spatial processing mechanism is activated for these unhealthy highly calorific items. By the same token, increasing the variety and environmental salience of low-calorie options (e.g. placing low-calorie instead of high-calorie items at check-out counters and other high-traffic areas) may steer food choice towards healthier alternatives, by enhancing their (perceived) convenience and essentially “levelling out” the inherent (perceived) search advantage of high-calorie foods – especially for

individuals in which the cognitive bias is greatest expressed (see **Chapter 4; Figure 7.1**). Indeed, there is growing support for the efficacy of such alterations to the physical (micro) food environment, or its corresponding choice architecture, in promoting healthy food consumption (Hollands *et al.*, 2019; van Kleef *et al.*, 2012; Pechey & Marteau, 2018).

In summary, a plethora of intervention opportunities – on both an individual and structural level – exists that can cater to specific components in behavioral pathways of the high-calorie spatial memory bias. Although proposed strategies may address upstream (*bias expression*) versus downstream (*bias translation*) processes to varying degrees of success individually (Hennessy *et al.*, 2020; Spring *et al.*, 2020; Turton *et al.*, 2016), the most desirable and sustainable outcomes are expected when a variety of techniques, which act on multiple levels, are used concurrently (Hofmann *et al.*, 2009; Johnson *et al.*, 2014).

7.5 Future Research Directions

Yet, pressing questions on the inner workings of the high-calorie bias in human spatial memory remain. Below, we delineate two distinct research lines that would be worthwhile to pursue on the scientific agenda for the cognitive bias.

7.5.1 Hijacking the spatial prioritization system to favor healthier food choices

Inspired by the philosophy of utilizing “flaws” in human decision making to advance desirable behavior (Thaler & Sunstein, 2008), future research should examine whether we are able to capitalize on the functional characteristics (i.e. calorie-sensitivity, automaticity, and efficiency; section **7.2.1**) of the spatial prioritization mechanism and use it to actively guide individuals towards healthier food choices.

More specifically, it is presently not entirely clear whether the high-calorie spatial memory bias responds to the *actual* or *perceived* caloric quality of a food, as the actual energy density of a food item was always congruent with (relative) perceptions of its caloric content in the majority of studies to date. The question therefore remains whether the prioritization of a food in spatial memory – according to its fitness relevance – is determined by its objective or subjective caloric content, during instances when the two aspects are dissociated from one another. There is evidence suggesting that the perception and experience of calories can be shaped by visual pre-ingestive cues (e.g. packaging labels), and resulting “top-down” expectations of the nutritional content of a

food are able to override its intrinsic nutritional properties in driving (post-ingestive) physiological responses (Crum *et al.*, 2011). Interestingly, the opposite trend in favor of actual caloric content has likewise been observed: Reward-related brain regions are differentially activated by food products similar in perceptual characteristics that only deviate on caloric content, upon and even prior to tasting (Frank *et al.*, 2008; Smeets *et al.*, 2011). Determining which tendency would apply most to the operations of the high-calorie spatial memory bias has yet to be done. The latter can be achieved with a lab-based experiment that manipulates perceived caloric content by varying nutritional labels on (calorie-matched) food products (e.g. Crum *et al.*, 2011). If it does prove possible to “hijack” the high-calorie bias in spatial memory to our advantage – by tricking our minds to develop an enhanced spatial memory for low-calorie products that are framed to be higher in caloric content – this could ultimately reduce the reliance of individuals on finite self-regulation resources to meet their healthy eating goals, especially in “tempting” situations of low self-control (cf. section **7.2.4**).

7.5.2 Optimizing behavioral insights and fine-tuning interventions on the high-calorie spatial memory bias

Another exciting avenue for future research relates to the optimization of intervention efforts targeting the cognitive bias. Although the usefulness of our proposed approaches (see section **7.4**) has yet to be ascertained in practice, these suggestions can be further supplemented with in-depth behavioral knowledge generated by methodologies that were not presently covered.

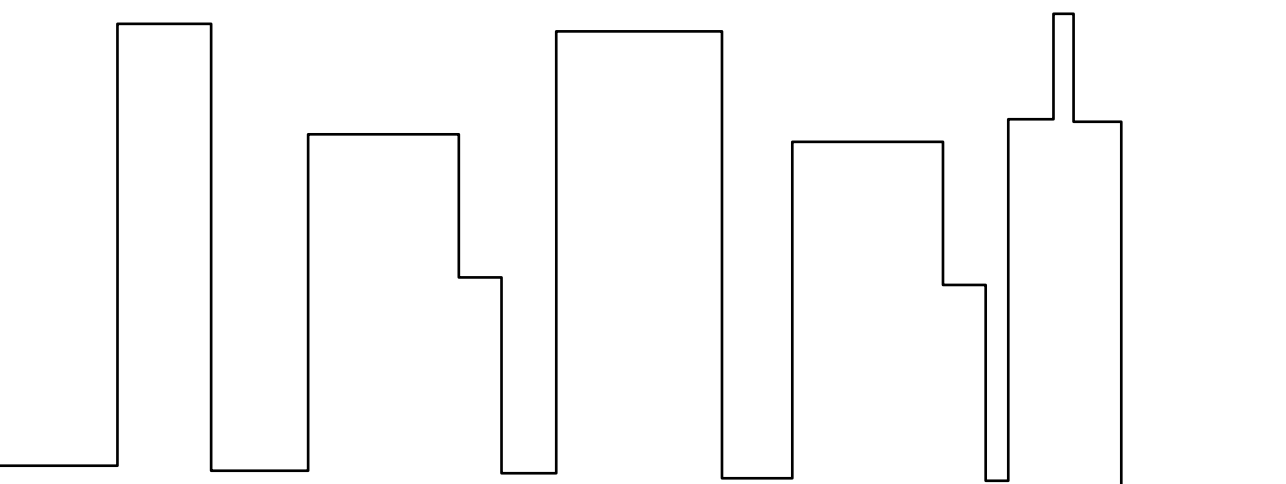
For instance, to finer decompose behavioral consequences of the high-calorie bias in human spatial memory, future studies could longitudinally track individuals’ eating behavior and food navigation in real-time using a smartphone application. GPS-based technology is available to monitor participants’ behavior and movements in large outdoor spaces (e.g. between food outlets), and a beacon-based equivalent can be used for tracking in smaller spaces (e.g. within a single food outlet) (Elliston *et al.*, 2017; McKay *et al.*, 2019; Poelman *et al.*, 2020; Spook *et al.*, 2013). These measurements would provide a rare spatiotemporal “blueprint” for an individual’s momentary food decisions (e.g. food purchases), as well as high-resolution (context-rich) insights into individuals’ extended eating patterns, both of which would facilitate the design of more personalized and ecologically-valid behavior change techniques.

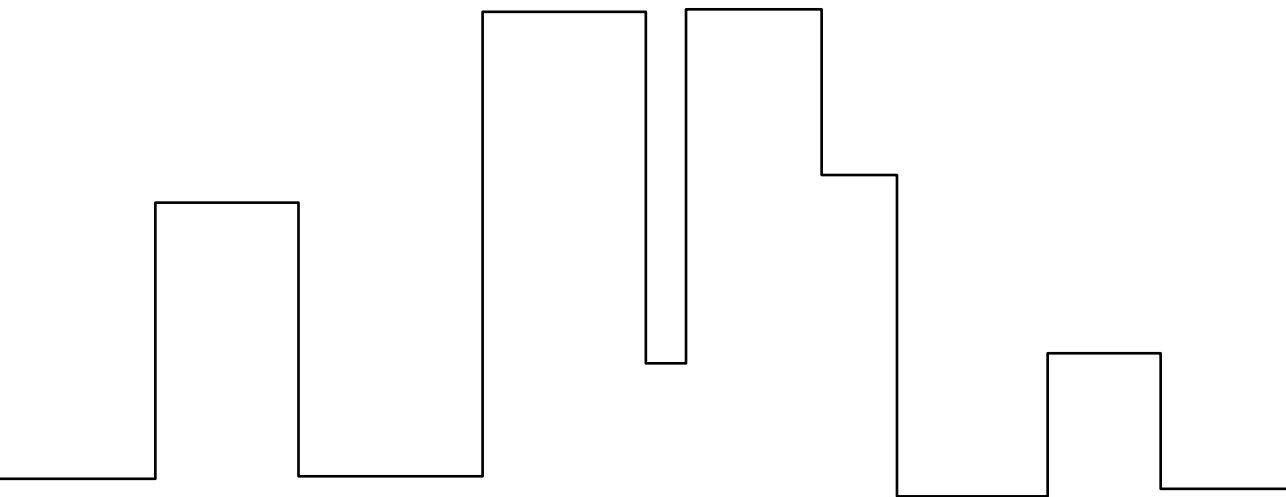
To this end, it would also be interesting to assess whether (and to what degree) the *overall* expression of the high-calorie bias in spatial memory changes in time and space, by repeatedly measuring individuals' food spatial memory at various times and physical locations across multiple days. Literature shows that an individual's valuations and preferences for a food are influenced by the immediate spatiotemporal context one makes food decisions in (e.g. one may prefer to eat high-calorie sweet foods such as cereal for breakfast at home in the morning; Cardello, 1994; Meiselman, 2006; Spence, 2021). Furthermore, hippocampal-dependent (spatial) memory function can be regulated by feeding-relevant endocrine systems (e.g. ghrelin and insulin concentrations), the latter of which fluctuate around mealtimes within a day (Suarez *et al.*, 2019). It is therefore reasonable to expect that the *overall* degree to which high-calorie food locations are prioritized in memory – averaging across all effects – could similarly exhibit a dynamic quality across spatiotemporal circumstances. If so, intervention strategies could use this information to concentrate treatment during certain “focal points” within a day, when the bias is typically highest expressed by an individual.

7.6 Concluding Remarks

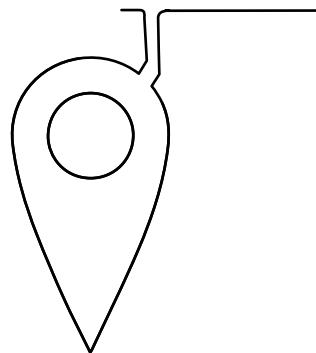
The present thesis provides compelling evidence for an inbuilt prioritization of high-calorie food locations in human memory. Importantly, this high-calorie bias in human spatial memory maladaptively influences how we navigate the modern food environment, by increasing the perceived ease of locating high-calorie foods, habitual high-calorie snack food purchases, visits to high-calorie food outlets, and individual BMI. Although diverse populations were all shown to express the spatial processing bias, individuals with a better ability to inhibit responding to high-calorie foods were protected from the bias' translation into undesirable dietary outcomes. Future research initiatives on the cognitive bias would benefit from incorporating more real-world methods to measure food spatial memory and capture individual eating behavior in “real-time” across spatiotemporal contexts. The effectiveness of proposed intervention techniques targeting the expression or behavioral translation of the high-calorie spatial memory bias should likewise be assessed in a broad participant demographic. In closing, human minds seem to be adapted for the efficient location and consumption of high-calorie foods within the harsh ancestral food environments in which we evolved.

Fine-tuning ways to mitigate unwanted tendencies of our “foraging minds” would bring us a step closer to promoting healthier eating behavior within our evolutionary-novel calorie-abundant food landscape.





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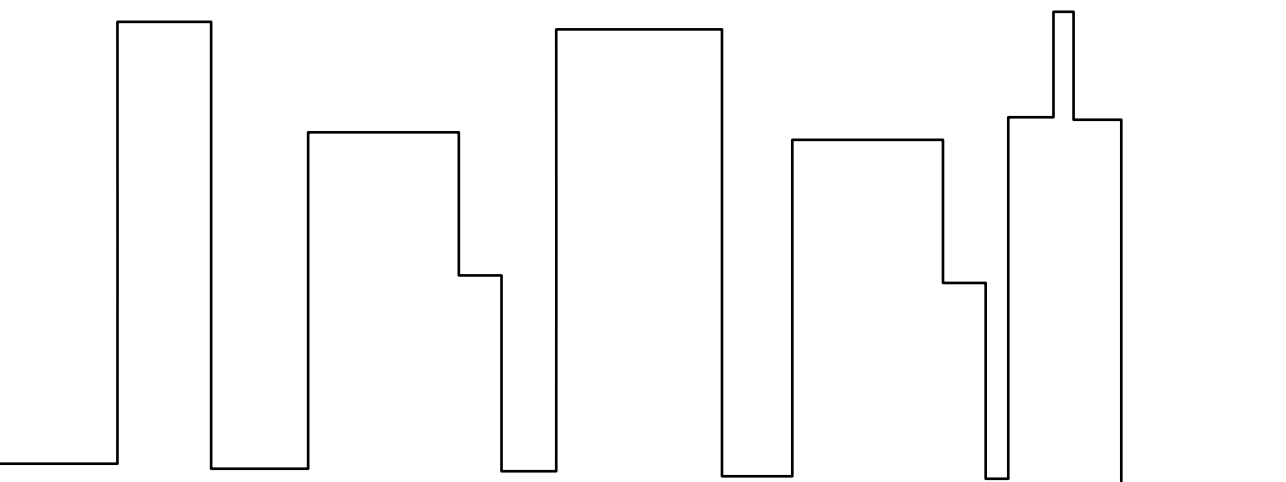
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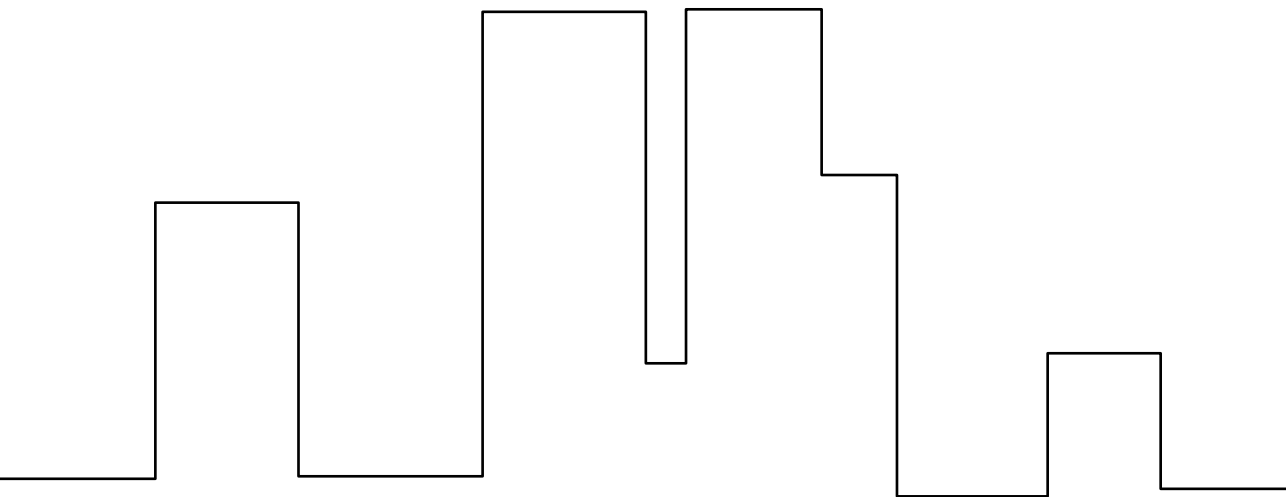
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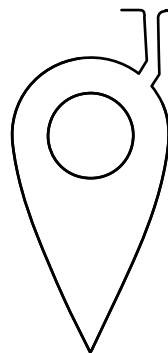
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Summary



The modern food environment is characterized by the proliferation of cheap, convenient, and highly palatable energy dense foods, stimulating the (over)consumption of ‘unhealthy’ high-calorie items (Egger & Swinburn, 1997; Hill *et al.*, 2003; Lakerveld *et al.*, 2018). However, not everyone overeats and develops a positive energy balance, indicating that large differences exist in how individuals respond to the heightened systemic availability and accessibility of high-calorie foods (Swinburn *et al.*, 2011; Small, 2009; Wardle, 2007). Identifying the factors that underlie these individual differences has become an important research theme within the fields of human eating behavior and health psychology, and has significant implications for (public) health promotion efforts and expenditures (Kortt *et al.*, 1998; Swinburn *et al.*, 2011). This thesis is grounded on the novel premise that differences in the ability to successfully navigate current “obesogenic” settings may (partially) stem from a cognitive adaptation that evolved for optimal foraging within harsh ancestral food environments. Specifically, from the *graded* expression of a calorie-sensitive cognitive system that enabled ancestral humans to efficiently (re)locate valuable nutritional resources with varying spatiotemporal availabilities – a *bias* in spatial memory for high-calorie foods (Allan & Allan, 2013; New *et al.*, 2007).

The overall aim of this thesis was to empirically examine the existence of a potential inbuilt prioritization, or “bias” in human spatial memory for high calorie foods, as well as its implications for individual eating behavior within a modern food environment. To this end, we devised the following five studies to systematically address both the *expression* and behavioral *translation* of a high-calorie bias in human spatial memory:

In **Chapter 2**, we first set out to rigorously investigate whether food-specific biases in human spatial memory are indeed expressed, across sensory modalities (i.e. vision and olfaction) of ecological significance to food navigation and food choice. We report on two controlled lab experiments featuring a computer-based spatial memory task with food images (Study 1; N = 88) and food odors (Study 2; N = 88), respectively. We also probed associations between food-specific biases in spatial memory and a range of (incidental and routine) eating-related parameters, in order to initially gauge their behavioral effects. We found that individuals more accurately recalled the locations of high-calorie and savory-tasting foods, while controlling for consciously mediated valuations or personal experiences with foods. However, the more accurate localization

of high-calorie foods did not differ for sweet or savory foods, or with an individual's trait eating style or degree of reward sensitivity. Furthermore, effects of biases in food spatial memory were not present on eating-related parameters of food preference, food choice, BMI, and waist circumference.

Chapter 3 describes an ambitious test for the existence of the high-calorie spatial memory bias outside of “sanitized” lab settings. To demonstrate the external validity of the bias, we carried out a large ($N = 512$) multisensory field-based experiment that allowed for two additional noteworthy elements: spatial navigation between distinct (three-dimensional) positions of food stimuli, and the incidental encoding of food locations. This format similarly enabled us to compare food spatial memory performance (and corresponding biases) between different sensory environments (i.e. multisensory conditions ($N = 258$) versus olfactory ($N = 254$) conditions). Overall, we found that individuals incidentally learned and more accurately recalled locations of high-calorie foods – regardless of explicit hedonic valuations or personal familiarity with foods. In addition, the high-calorie spatial memory bias was equally expressed in both sensory environments – even where solely odor information was available.

Chapter 4 improves upon previous lab-based paradigms (cf. **Chapter 2**) to assess the behavioral translation of the high-calorie spatial memory bias, by utilizing a real-world food environment. In a lab-plus-field experiment, we investigated the bias' effects on the food search and food choice of 60 individuals navigating an unfamiliar supermarket. Across two test sessions, participants first performed eye-tracking and spatial memory tasks in a lab setting, and then completed food search and (covert) food choice tasks in a supermarket. Although individuals were faster at localizing high-calorie versus low-calorie foods in the supermarket, the high-calorie spatial memory bias did not predict a lower search time for high-calorie foods, or a higher proportion of high-calorie food choice. In addition, expression of the high-calorie bias in spatial memory was not associated with a bias in attention for high-calorie foods. Rather, an enhanced memory for high-calorie food locations was associated with a lower perceived difficulty (i.e. greater ease) of finding high-calorie items in the supermarket, which may potentiate later choice of a high-calorie food.

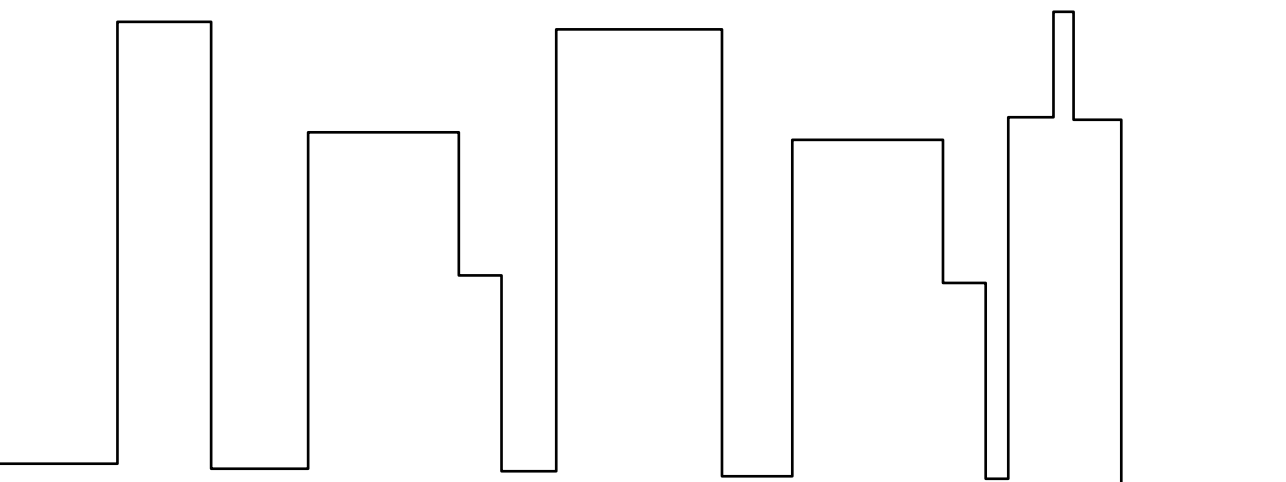
In **Chapter 5**, our focus was on implications of the high-calorie spatial memory bias for individuals' *routine* (repeated) eating behavior, to gain insights on top of that provided by more *incidental* (single-instance) measures (cf. **Chapters 2 and 4**). In an

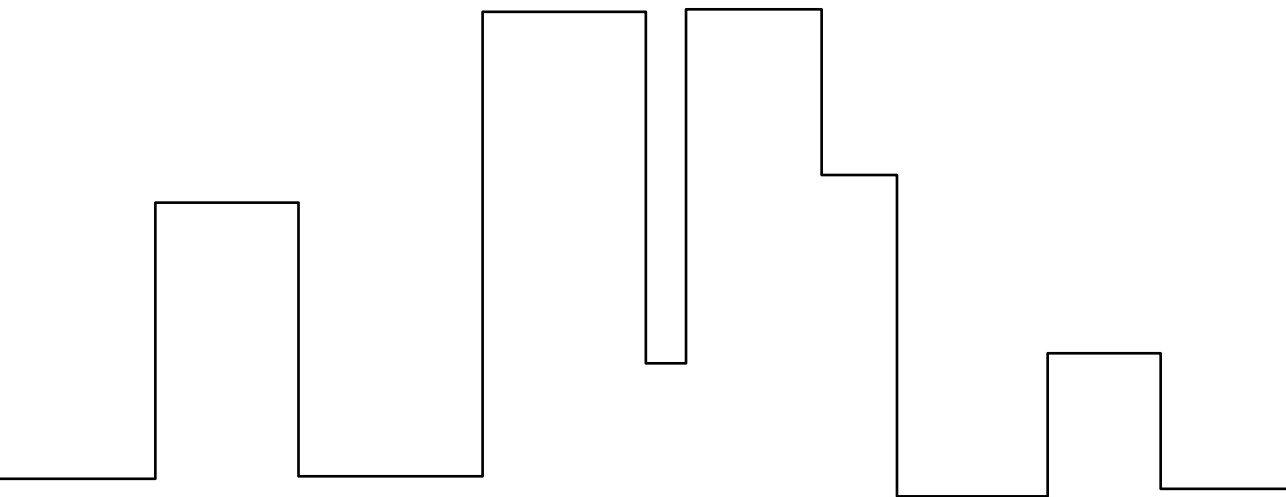
online study, we tested the food spatial memory of a diverse sample of 405 individuals, as well as examined associations between the high-calorie spatial memory bias and the routine frequency of high-calorie snack consumption, exposure to high-calorie food environments, and BMI of a subset of 316 individuals. For the latter, we assessed individual psychological factors (e.g. snack purchasing habits, inhibitory control) that could either synergize or antagonize the bias' behavioral effects. A greater expression of the high-calorie spatial memory bias predicted a stronger habit of purchasing high-calorie snack foods and consequently a higher individual BMI. Although individuals from various sociodemographic groups expressed the high-calorie bias in spatial memory, our results demonstrate that those with a better inhibitory control to high-calorie foods were protected from bias-induced tendencies to frequent high-calorie food outlets.

Chapter 6 questions whether the high-calorie bias in spatial memory represents a universal cognitive mechanism and can be reasonably generalized to individuals from varying cultures. Through the means of a cross-cultural online experiment (and data from **Chapter 5**), we measured and compared the food spatial memory of diverse populations from the USA (N = 72), Japan (N = 74), and the Netherlands (N = 405) using a standardized computer-based spatial memory task. We demonstrate that individuals native to cultures that diverge on relevant cognitive characteristics, built food environments, and food attitudes were effectively identical in their food relocation performance: Locations of resources with a higher caloric quality were more accurately recalled than that of low-calorie alternatives to a similar degree across countries, regardless of individuals' hedonic preferences and familiarity with foods, or explicit effort to encode food locations. The high-calorie bias in spatial memory was also uniformly expressed by diverse sociodemographic groups within a population.

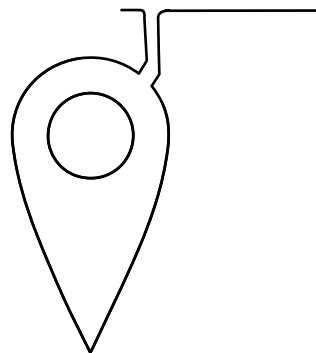
In conclusion, the work described in this thesis provides compelling evidence for an inbuilt prioritization of high-calorie food locations in human memory. Importantly, this high-calorie bias in human spatial memory maladaptively influences how we navigate the modern food environment, by increasing the perceived ease of locating high-calorie foods, habitual high-calorie snack food purchases, visits to high-calorie food outlets, and individual BMI. Though diverse populations were all shown to express the spatial processing bias, individuals with a better ability to inhibit responding to high-calorie foods were protected from the bias' translation into undesirable dietary

outcomes (i.e. increased visits to high-calorie food outlets). Future research initiatives would benefit from incorporating more real-world methods to measure food spatial memory and capture individual eating behavior in “real-time” within multiple spatiotemporal contexts. In closing, human minds seem to be adapted for the efficient location and consumption of high-calorie foods within the harsh ancestral food environments in which we evolved. Fine-tuning ways to mitigate unwanted tendencies of our “foraging minds” would bring us a step closer to promoting healthier eating behavior within our evolutionary-novel calorie-abundant food landscape.





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Guido, thank you for helping me navigate academic hurdles ever since the *good ol' days*, when I was a (naive) MSc thesis student assisting you with data collection. You have always looked out for me, and I wish to one day harness your superhuman nerves of steel and lightning-quick strategizing powers. You are by far the coolest (living) artefact of all time, and you make a mean tomato meatball sauce. *Now, sashay away.*

Maria SC, you are the embodiment of when sweetness and strength meet. I will never forget our late-night hours (or dinners) together at the office, hearing *Highway to Hell* blast out from your earphones, or your incredible – and often hilarious – life stories. I will miss having you as a seatmate. Let's go out dancing soon with **Tsitsi**!

Matjaz & Eva C, a wise couple once told me "too much pi gives you a wide circumference". I am happy to have met like-minded individuals at the office, who have a mutual appreciation for herbs, pizza, eastern (or geographically central) European spirits, and cringey YouTube videos. I am glad that I got to know you both as individuals, as well as fun colleagues.

My PhD experience was further enriched by other SSEB and HNH colleagues: **Apple, Arli, Asrul, Carlos, Charlotte K, Elbrich, Elise, Erna, Eva K, Giulia, Inge G, Inga, Janneke, Koen, Korrie, Marielle, Maria D, Maria J, Marion, Marlou, Naomi, Roelien, Ruoxuan, and Tsitsi**. Many thanks to you all for the nice lunches, coffee breaks, and shared PhD activities.

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Of course, my adventure would not have been complete without fellow CHL colleagues. Although the majority of my time was spent at HNH, I always felt welcome and at home at the department. CHL's online borrels, cocktail workshops, and team-building events remain unbeatable :-)

Merije and **Stas**, thank you for being awesome first roomies when we were a “small” group of Emely’s PhDs at COM. I vividly remember the amount of sweets we kept in that office, which were luckily locked away in a drawer (in case of emergencies) ;-)

Sofie and **Sanne R**, you are indeed the original PhDs and “guardians” of the group. Thank you for always lending a helping hand, and for being up for fun coffee breaks. I look back on our Lebo lunches fondly.

Angeliek, you were for a large part living in “the land down under”, but you were an absolute superstar teammate at Lowlands!

Hanneke, Lean, and Thirza: Funnily enough, I got to know you all better during lockdown. Thank you for all the fun online PhD games and *gezelligheid*!

Nanako, thank you for helping out with my cross-cultural experiment. Your feedback went a long way!

To all the **newer CHL PhDs**: it was a short but sweet introduction. I look forward to getting to know each of you better in the coming period :-)

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To my past supervisors and mentors – **Bas Engel, Gerry Jager, Liesbeth Zandstra** – thank you for opening doors for me early on in my academic career. I have certainly learned a lot from each one of you, and I am happy that we managed to capture our respective research collaborations in nice publications.

I was fortunate enough to not have *one* but *two* teams of supporting staff to help me out with the painful logistical side of academia. To these lovely essential figures who operate from behind the scenes – **Anne van de Wiel, Ayla S, Cathelijne Goossens, Corine Perenboom, Els Siebelink, Gea Brussen, Inge Ru, Jasmijn Mater, Lidy de Vreede, Ria Meurs, Riekje Janssen**, and **Vera Mentzel-Dikker Hupkes** – thank

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Zahabia, *started from the bottom* (i.e. glucose tolerance lab practicals) *now we here!* From MSc study/party nights to our mini-reunion in Canada last year – thank you for your continued support throughout the years.

Alver, Calvin, Eno, Ivan, Milla, Patricia, Tara, and **Tariq**: Thank you for making time for me whenever I visit home (and/or for visiting me on your Euro-trips!). Our long-lasting friendships mean a great deal to me.

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Gaby, my sister from another mister. Our Barcelona trip was one of the absolute highlights of the past few years, and is just a taste of the woodland holidays to come. I

am so proud of us for sticking together since our beginnings as awkward mixed kids in the concrete jungles of Jakarta. Though we may not get to meet as often, we so easily pick up from right where we left off every time. Until soon my little *nasta*!

Kegan, Monice, and Tes: My NL girlies! It still astounds me how far we all have come since our instant-brownie movie nights, Outrageous dance training days, and Havana/Zussen parties out at UCU. I consider myself one remarkably fortunate gal to be closely surrounded with such internationally-oriented, high-powered, and ambitious positive women. **Jasper, Sander P, and Thijs,** I am glad that you make up the remainder of the FOMO group, because we never run out of interesting conversation or comedy material with you guys around :-)

Uncle Mochtar and Tante Sherida, the line between “nuclear” and “extended” family was always blurry with us, which is a testament to the warm, open, and honest connections you two provide. Thank you for being a pillar of support whenever it was needed. You both have taught me a lot on choosing authenticity and following my own happiness. **Roman and Raffy,** though you two are technically my “younger cousins”, you definitely act more like big brothers. Thank you for having my back and for always being up for a fun night! **Joy,** I am so glad to have you as part of the family :-)

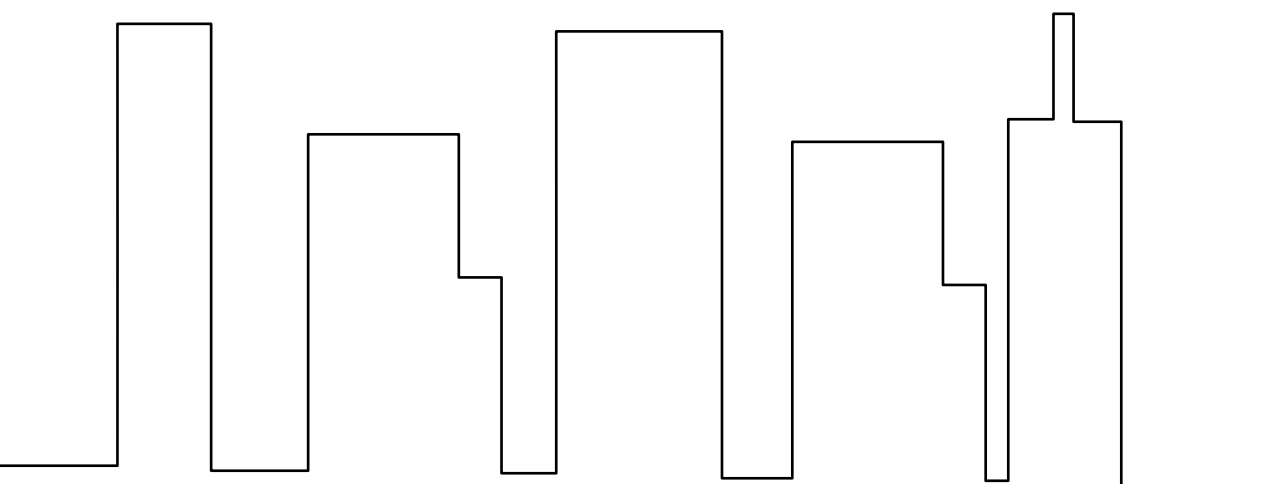
Oma, thank you for being the prime example of resilience and kindness during tough moments, and to not take life too seriously sometimes. You are still the only person that I can talk and laugh in 3 different languages with, simultaneously (*Kepala Chipi jangan jadi terlalu besar ya*). I cherish our bond and all the memories shared with you (and **Gerard!**). Ik hou van je!

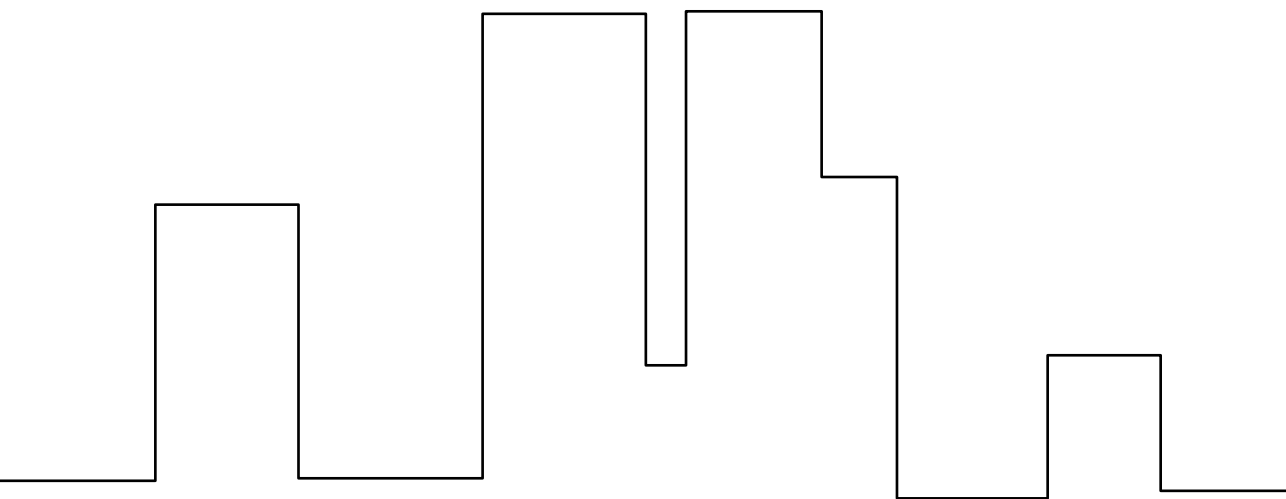
Isabella, how lucky am I to have you as my lead cheerleader! I love how we can always be 100% sincere with each other, and fully understand one another’s humor. It swells me up with pride when I think about how much we both have grown personally and professionally, as well as how we continue to hold space and grace for family despite living busily in separate time zones. **Pete,** you too have become part of my support system and I have come to the conclusion that there is no such thing as a dull (i.e. quiet) night out with you. Thanks for adding some *masala* into our mix (*innit*).

Mom and Dad, my achievements are nothing but a reflection of your years of hard work, grounded in unconditional love and the drive to provide **Isa** and I with the best possible opportunities to pursue our passions. From the neon purple school uniforms of RICS, annual moving-out days at UCU, to dealing with paper rejections during my PhD: **Mom**, thank you for being such a big comforting beam of sunshine through it all. You never fail to remind me of my roots and of never losing my inspiration. I definitely get my inner strength and bubbiness from you. **Dad**, your fondness of classy dinner parties, Murphy's law, properly-executed *gado gado*, and Hendrix's guitar riffs will always be cherished. *Terima kasih*. I am forever grateful to (for) you both.

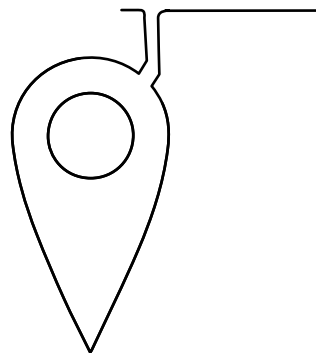
And finally, to Pol: I never would have thought at the beginning of my PhD that I would be reserving the final paragraph of my Acknowledgments for you*. But I am so grateful that this has become our reality, and that we shared these literal chapters of our lives together. Thank you (and your patience!) for teaching me that loving someone can be so easy if you are with the right person. Thank you for welcoming me into your warm and wonderful family. I could not have asked for a more intelligent, witty, compassionate, and hot life partner; I am the happiest and best version of myself when I am with you. I love you, *sayang*, let's own our wildest dreams.

**and our fluffball Bowie*





About the Author



About the Author



Rachelle Joanna de Vries was born on August 8, 1993 to a Dutch-Chinese father and Filipina mother in Jakarta, Indonesia. She obtained her secondary school diploma on scholarship from Raffles International Christian School in Jakarta, where she received an award for the most distinctions in the Cambridge A-level examinations (2011). After, Rachelle moved to the Netherlands to attend University College Utrecht – the international honors undergraduate program of Utrecht University – where she received her BSc degree (*cum laude*) with a major in

Biochemistry and a minor in Psychology (2011-2014). During this period, Rachelle became increasingly passionate about psychobiological determinants of health, and conducted her thesis on the interaction between genetic and prenatal environmental risk factors for ADHD severity at the university hospital of Utrecht (*UMCU*). Soon after completing her undergraduate education, Rachelle enrolled into the Nutrition and Health MSc program at Wageningen University & Research (2014-2016), where she fell down the wonderful rabbit hole of sensory science and eating behavior research. Her Master's degree culminated with an internship at Unilever R&D (Vlaardingén), where she investigated haptic- and visual-based digital strategies to stimulate healthier online food choice. Rachelle also worked as a teaching assistant in a Master-level Advanced Statistics course from the *Biometris* group of Wageningen University, for a total of six months (in 2016) during her postgraduate period.

In 2017, Rachelle started as an “interdisciplinary” PhD candidate at the Division of Human Nutrition (Sensory Science and Eating Behavior) and Consumption and Healthy Lifestyles departments of Wageningen University & Research. Her PhD project nicely intersected her affinities for sensory science, cognition, and health psychology. During her PhD appointment (March 2017-2021), Rachelle regularly assisted in teaching Bachelor- and Master-level courses, supervised BSc and MSc research projects, and actively disseminated research findings at various international scientific conferences and media outlets. In addition, she was a member of the organizing committee (sponsoring team) of the Human Nutrition PhD research exchange to Canada in 2019.

As of August 2021, Rachelle works as a lecturer/researcher at the Consumption and Healthy Lifestyles department of WUR, where she continues to practice her passion for eating behavior research, data science, and health promotion.

Publications in peer-reviewed journals

de Vries, R., Boesveldt, S., & de Vet, E (2021). Locating calories: Does the high-calorie bias in human spatial memory influence how we navigate the modern food environment? *Food Quality and Preference*, 104338. <https://doi.org/10.1016/j.foodqual.2021.104338>

de Vries, R.*, Morquecho-Campos, P.*, de Vet, E., de Rijk, M., Postma, E., de Graaf, K., Engel, B., & Boesveldt, S. (2020). Human spatial memory implicitly prioritizes high-calorie foods. *Scientific Reports*, 10(1), 1-6. <https://doi.org/10.1038/s41598-020-72570-x>. *Shared first authorship

de Vries, R., de Vet, E., de Graaf, K., & Boesveldt, S. (2020). Foraging minds in modern environments: high-calorie and savory-taste biases in human food spatial memory. *Appetite*, 152, 104718. <https://doi.org/10.1016/j.appet.2020.104718>

de Vries, R., Jager, G., Tijssen, I., & Zandstra, E. H. (2018). Shopping for products in a virtual world: Why haptics and visuals are equally important in shaping consumer perceptions and attitudes. *Food Quality and Preference*, 66, 64-75. <https://doi.org/10.1016/j.foodqual.2018.01.005>

Submitted for publication

de Vries, R., Boesveldt, S., & de Vet, E. Human spatial memory is biased towards high-calorie foods: A cross-cultural online experiment.

de Vries, R., Boesveldt, S., Sotomayor Sainz, A., Copier, J., & de Vet, E. Wired for harsh food environments: Human spatial memory favors the effortless location and consumption of high-calorie foods.

Abstracts and presentations

de Vries, R., de Vet, E., de Graaf, K., & Boesveldt, S. (2020). The high-calorie bias in human spatial memory lowers the perceived difficulty of finding high-calorie foods in an unfamiliar supermarket environment. Poster presentation at the Eurosense conference, Online.

de Vries, R., de Vet, E., de Graaf, K., & Boesveldt, S. (2019). Foraging minds in modern environments: High-calorie and savory-taste biases in odor-cued food spatial memory. Poster presentation at the British Feeding and Drinking Group (BFDG) annual meeting, Swansea, UK (awarded a bursary).

de Vries, R., de Vet, E., de Graaf, K., & Boesveldt, S. (2019). Evolutionary tendencies: Multisensory investigations into human food spatial memory biases. Oral presentation at the Women In Olfactory Science (WIOS) conference, Wageningen, the Netherlands.

de Vries, R., Boesveldt, S., de Graaf, K., & de Vet, E. (2018). Evolutionary tendencies: the potential role of a high-calorie bias in food spatial memory on eating behaviour. Oral presentation at the Food for Future Symposium, Wageningen, the Netherlands (invited talk).

de Vries, R., Boesveldt, S., de Graaf, K., & de Vet, E. (2018). Evolutionary tendencies: The potential role of a high-calorie bias in food-specific spatial memory on eating behaviour. *Abstracts/Appetite*, 130, 296-320. <https://doi.org/10.1016/j.appet.2018.05.180>. Oral presentation at the British Feeding and Drinking Group (BFDG) annual meeting, Lyon, France (awarded a bursary).

Media interviews: highlights

New Scientist (2021). Mensen onthouden onbewust beter waar calorierijk voedsel te vinden is. <https://www.newscientist.nl/nieuws/mensen-onthouden-onbewust-beter-waar-calorierijk-voedsel-te-vinden-is/>

The New York Times (2020). Where'd I Stash That Chocolate? It's Easy to Remember. <https://www.nytimes.com/2020/10/13/well/eat/chocolate-memory-mind-psychology-calories.html>

Scientias.nl (2020). De locatie van een zak chips onthouden we gemakkelijker dan de locatie van een komkommer. <https://www.scientias.nl/de-locatie-van-een-zak-chips-onthouden-we-gemakkelijker-dan-de-locatie-van-een-komkommer/>

Scientific American (2020). Our Brain Is Better at Remembering Where to Find Brownies Than Cherry Tomatoes. <https://www.scientificamerican.com/article/our-brain-is-better-at-remembering-where-to-find-brownies-than-cherry-tomatoes/>

Overview of completed training activities

Discipline specific activities	Organizer and location	Year
<i>Courses</i>		
NutriScience – A Multifaceted Approach to Nutrition Research	VLAG, Wageningen, NL	2017
Summer School on Human Olfaction	Smell & Taste Clinic, Dept of Otorhinolaryngology, University of Dresden Medical, Dresden, DE	2017
Sensory Perception & Food Preference: The Role of Context	VLAG, Wageningen, NL	2018
Masterclass Food Environments	KNAW, Amsterdam, NL	2019
Tobii Eye-tracker Training	Tobii Sweden, Wageningen, NL	2019
Burghart Olfactometer Training	Burghart and WUR, Ede, NL	2020
<i>Conferences and meetings</i>		
Women In Olfactory Science (WIOS) Conference	WIOS, Trieste, IT	2017
WINK – The Nudge Conference	WINK (NWO, Utrecht University & WUR), Utrecht, NL	2017
The Netherlands Olfactory Science Exchange (NOSE) First Scientific Meeting	NOSE, Utrecht, NL	2017
The British Feeding and Drinking Group (43 rd annual meeting) - <i>Oral presentation</i>	BFDG, Lyon, FR	2018
Women In Olfactory Science 2nd Conference - <i>Oral presentation</i>	WIOS, Wageningen, NL	2019
The British Feeding and Drinking Group (44 th annual meeting) - <i>Poster presentation</i>	BFDG, Swansea, UK	2019
Eurosense: 9th European Conference on Sensory and Consumer Research - <i>Poster presentation</i>	Eurosense, Online	2020
General courses		
VLAG PhD week	VLAG, Wageningen, NL	2017
Introduction to R	VLAG, Wageningen, NL	2017
Applied Statistics	VLAG, Wageningen, NL	2018
Generalized Linear Models	PE&RC, Wageningen, NL	2018

About the Author

WGS PhD Carousel 2018	Wageningen Graduate Schools, Wageningen, NL	2018
Scientific Writing	Wageningen In'to Languages, Wageningen, NL	2018
Advanced Qualitative Research Design & Data Collection	WASS, Wageningen, NL	2019
PhD Pitch Training	Human Nutrition and Health WUR, Wageningen, NL	2019
Writing Grant Proposals	Wageningen Graduate Schools	2020
Other activities		
Preparing PhD Research Proposal	WUR, Wageningen, NL	2017
Human Nutrition and Health Department Meetings	WUR, Wageningen, NL	2017- 2021
Consumption and Healthy Lifestyles Department Meetings	WUR, Wageningen, NL	2017- 2021
Edema-Steernberg Foundation Annual Meetings	WUR, Wageningen, NL	2017- 2021
Edema-Steernberg Foundation Literature Discussion Group	WUR, Wageningen, NL	2017- 2021
Principles of Sensory Science I (HNE- 30506)	WUR, Wageningen, NL	2017
PhD Tour 2019 (+ organizing committee)	Human Nutrition and Health WUR, Wageningen, NL	2018- 2019
Food for Future Symposium – <i>Invited</i> <i>Talk</i>	WUR, Wageningen, NL	2018
Worldwide Wageningen Alumni Reunion – <i>Foodlab Stand</i>		

Colophon

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